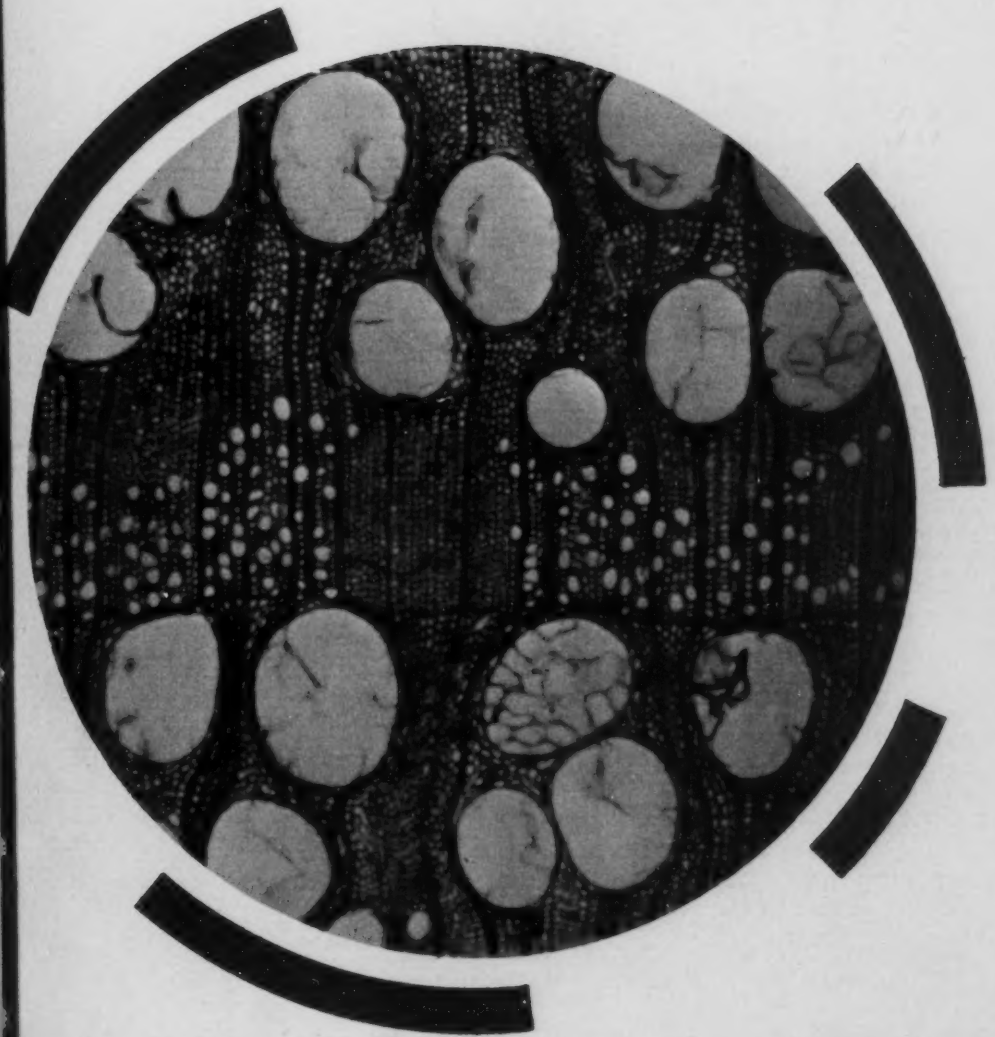
A Quarterly Journal of Research and Technical Progress

FOREST *Science*



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The cover design is a microphotograph of American elm in transverse section by Stephenu B. Preston, University of Michigan.

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Effect on Streamflow of Cutting a Forest Understory

BY
EDWARD A. JOHNSON
JACOB L. KOVNER

FOR SMALL HEADWATER drainages or watersheds, the water loss to the atmosphere through evapotranspiration (including interception) is influenced by changes in vegetation characteristics and root depth. Various artificial devices such as lysimeters have been used to measure evapotranspiration directly and have provided comparative data for herbaceous plants, grass, and agricultural crops. Comparative data for trees, however, are extremely difficult to obtain by these methods.

Since trees occur on the headwaters of many streams, there is considerable interest in watershed experiments involving measurement of forest cover, precipitation, and streamflow, particularly where the data afford a measure of evapotranspiration. Publications by Hoover (1944), Dunford and Fletcher (1947), Lieberman and Hoover (1951), the Southeastern Station (1953), Johnson and Kovner (1956), and Kovner (1955) report on changes in streamflow following the cutting of forest vegetation at the Coweeta Hydrologic Laboratory in the mountains of western North Carolina.

This paper deals with the effects upon streamflow of cutting a dense understory of laurel and rhododendron on a forested watershed at the Coweeta laboratory. The paper also describes later changes in flow as the understory was allowed to grow back.

An understory of mountain-laurel (*Kalmia latifolia* L.) and rosebay rhododendron (*Rhododendron maximum* L.) is associated with hardwood stands on 1½ million acres in the Southern Appalachian Mountains. Generally, mountain-laurel occupies the drier sites such as ridges and south-facing slopes, while rosebay rhododendron is found on north slopes and along streambanks. The common shrubby understory averages around 10 feet in height, although an arborescent form may reach a height of 25 feet, with stems up to 9 inches d.b.h. (Fig. 1). The foliage is evergreen and extensive and the roots are concentrated in upper layers of the soil.

During the growing season the dominant canopy of trees intercepts the major portion of the incoming solar radiation, and wind movement is reduced near the ground. Under these conditions it is not easy to estimate the contribution to the over-all water loss made by the understory vegetation. Forest managers recognize laurel and rhododendron as economically worthless and favor removal of this aggressive competitor with valuable timber.

The authors are Foresters at the Southeastern Forest Experiment Station, Forest Service, U. S. Dept. of Agriculture. They are assigned to the Coweeta Hydrologic Laboratory, Franklin, N. C.

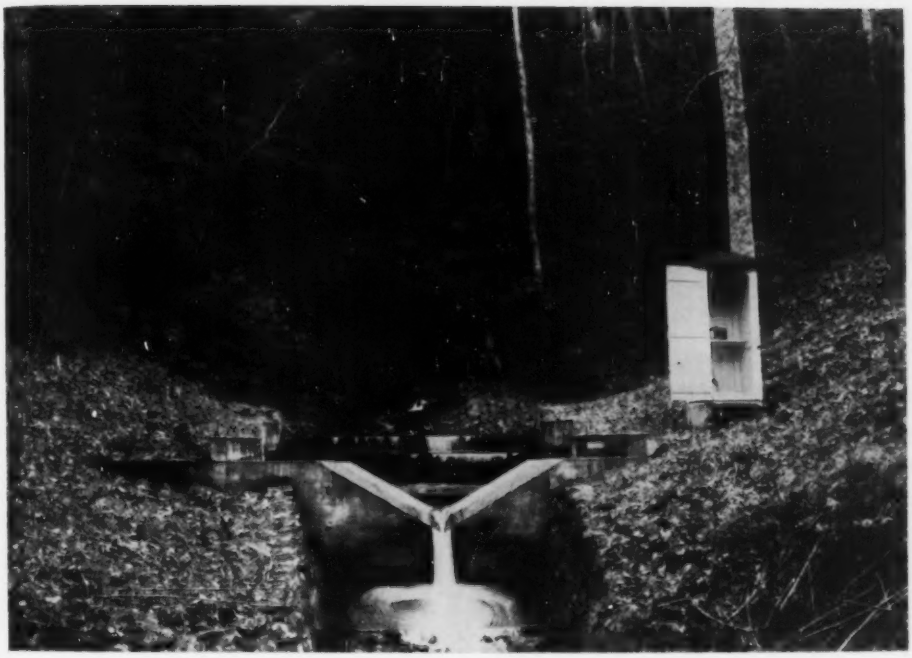

FIGURE 1. *Arborescent form of rhododendron on the treated watershed before cutting. Stream gaging station in foreground.*

Methods

The procedure for an experimental watershed study at the Coweeta Hydrologic Laboratory begins with a period of calibration, which includes measuring streamflow and precipitation (Kovner and Evans, 1954). Vegetation is mapped and inventoried and a soil survey is made. The vegetative cover is then changed and the same streamflow and precipitation measurements continued. A control watershed under natural conditions is permanently used as a reference check area to provide a means by which variation due to climate and other factors not associated with the treatment may be minimized. From these records it is possible to determine the effect on streamflow of cutting forest vegetation (Wilm, 1949). In this particular study, watershed 19 was selected for treatment, and watershed 21 was the control, as shown in Figure 2.

The Experimental Watersheds

These watersheds are located in the Nantahala Range of the Southern Appalachian Mountains near Franklin, North Carolina. The mountains are made up principally of crystalline rocks of pre-Cambrian age. Locally the country rock consists of various kinds of granitic mica schists and gneisses, principally the so-called Carolina gneiss. The area is free of extensive faulting and the truly massive underlying rock formations are considered watertight. All soils have been derived from weathering of underlying acid crystalline rock formations to form a relatively deep soil mantle, which is often penetrated to a considerable depth by tree roots.

On steep slopes, the soil mantle averages 3 feet in depth. The surface soil ranges from 4 to 6 inches in depth and consists of a mellow, friable, brown loam. The subsoil varies from 30 to 40 inches and consists of a friable, crumbly, reddish brown clay loam.

In the coves and at the base of slopes the soil varies from 4 to 18 feet in depth. The surface soil, a sandy loam, ranges from 1 to 3 feet in depth and varies from black to dark brown in color, with a high content of organic matter. The subsoil sandy clay loam varies from 3 to 15 feet, with roots penetrating the soil mass to a depth of 6 to 7 feet. Large amounts of angular stones and rock fragments are mixed throughout the soil profile.

The infiltration capacity of the soils is high, reflecting good structural development and internal drainage. In this connection it is important to note that on the two study watersheds no overland flow that would move litter on the forest floor has ever been observed.

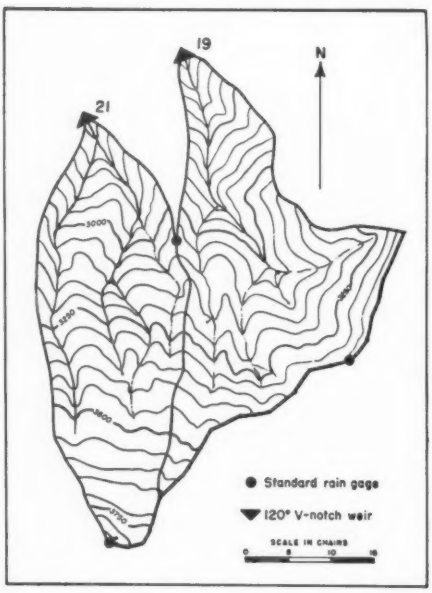

FIGURE 2. *Topographic map of the 70-acre watershed 19 (treated) and the 59-acre watershed 21 (control).*

The climate is perhumid, according to Thornthwaite's (1948) classification. The mean annual temperature is 55° F., and the growing season extends from April 19 to October 22. Winter temperatures are variable, with frequent periods of 65 to 70° F., and periods of subfreezing temperatures. There is a marked consistency in temperature during the summer, in contrast with variations experienced from year to year in other seasons. The abundant precipitation and warm temperatures favor plant growth, and transpiration is seldom limited by drought.

Based on a 15-year record, the average annual rainfall on the treated watershed is 80 inches, with extremes of 67 inches and 98 inches for individual years. The mean precipitation on the control is 82 inches, with a range of 69 to 100 inches. Less than 2 percent of the annual precipitation occurs in the form of snow.

Before treatment, average annual streamflow was 48 inches and 52 inches on the treated and control watersheds, respectively. About 8 percent of annual streamflow was stormflow and 92 percent from groundwater.

The regional forest type on the areas at time of treatment was largely oak-hickory (Fig. 3). It was a well-stocked stand having no large breaks in the crown canopy, with a crown density around 0.85. A tally of stems larger than 0.5 inches d.b.h. indicated that the forest stand on the treated watershed had a basal area of 114 sq. ft. per acre distributed as follows: deciduous trees 87, conifers 2, rhododendron 11, and laurel 14.

Between December 28, 1948, and March 2, 1949, all laurel and rhododendron growing on the 70-acre treated watershed were cut as close to the ground as possible with hand tools and with minimum disturbance to the soil and litter cover. Time required for cutting was 4

TABLE 1. Distribution of the laurel and rhododendron understory vegetation by regional forest types on watershed 19

Regional type	Area in type	Understory vegetation		
		Rhododendron	Laurel	None
	Acres	*Acres*	*Acres*	*Acres*
Oak–hickory	61	18	27	16
Cove–hardwood	8	8	0	0
Yellow–pine hardwood	1	0	1	0
Total	70	26	28	16

man-days per acre. Twenty-six acres (Table 1) were a relatively pure stand of rhododendron, 85 to 100 years old, with stems up to 9 inches d.b.h.

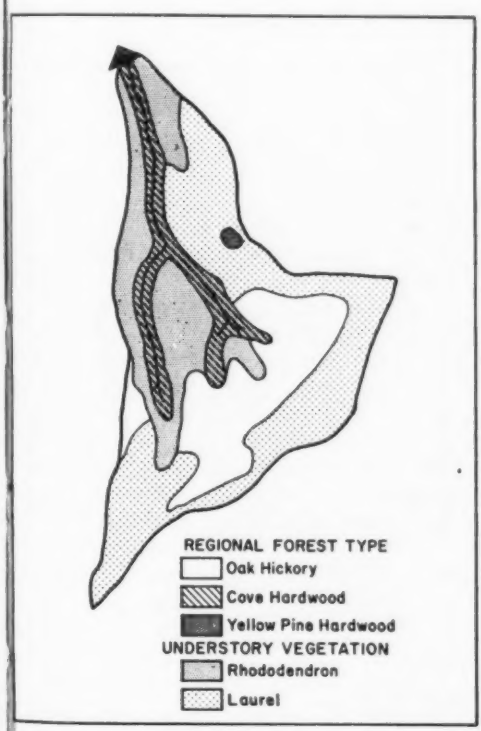

FIGURE 3. *Forest canopy and understory type map at time of treating watershed 19.*

Branches from the larger shrubs were lopped and scattered. With this exception, slash was left as it fell and no attempt was made to keep it out of stream channels. Leaves on the cut stems did not begin to drop until the latter part of the first summer. Even after 2 years, many of the smaller branches still remained firmly attached to the cut vegetation. No cutting of the regrowth has been undertaken. Growth from stumps has been very slow, and by 1955 average height of the sprouts was only 30 to 36 inches (Fig. 4).

Results

Annual Streamflow

Annual precipitation and streamflow data for the treated and control watersheds are given in Table 2. The data are arranged by 12-month periods which begin May 1 and end April 30. This particular hydrologic year was selected because it gives the best correlation between streamflow variables (Lieberman and Fletcher, 1947). The year 1948-49, during which cutting took place, has been omitted because it included both pretreatment and treatment values.

Effect of the cutting treatment on streamflow from watershed 19 may be determined by significance of difference between adjusted mean annual streamflows for the pretreatment and treatment periods. The analysis of covariance (Snedecor, 1946) as applied to the data in columns 4 and 5 of Table 2, showed that the

TABLE 2. Annual streamflow and precipitation in area inches for the period May 1 to April 30.

Year	Precipitation		Streamflow	
	Control	Treated	Control	Treated
	PRETREATMENT PERIOD			
1941–42	69.16	66.87	42.58	38.52
1942–43	89.93	87.93	60.42	55.44
1943–44	86.02	84.94	58.15	54.24
1944–45	71.27	69.86	42.13	39.28
1945–46	85.92	84.02	60.88	55.43
1946–47	73.39	71.85	46.92	44.02
1947–48	80.82	79.46	54.03	49.49
Average	79.50	77.85	52.16	48.06
	TREATMENT PERIOD			
1949–50	94.94	92.94	75.47	73.14
1950–51	79.36	76.88	50.86	49.28
1951–52	89.42	87.01	63.94	61.34
1952–53	71.67	70.70	44.08	41.52
1953–54	81.15	79.55	48.14	45.87
1954–55	70.12	68.94	41.67	39.18
Average	81.11	79.34	54.03	51.72

variances are homogeneous, and regression coefficients are not significantly different at the 1-percent level. The regression lines for the two periods will, therefore, be considered parallel, and the test of significance for distance between the two lines may be carried out. This analysis showed the adjusted difference amounts to 1.85 inches, which is significant at the 1-percent level with limits of 0.57 to 3.14 inches. This is a 4-percent increase based on the expected mean annual streamflow for the 6-year treatment period.

FIGURE 4. *Four years after cutting, laurel sprouts had grown only 24-30 inches high. Uncut laurel is shown at upper left.*

Because of the nature of the treatment, as will be noted later, the estimated annual increases for each year of the treatment period require further examination. An estimated annual increase in streamflow is obtained as the difference between the observed streamflow value for a given year and the corresponding estimate calculated from a regression which is based upon pretreatment period data in Table 2, and given by:

$$Y = 0.8040 + 0.9060X \qquad (1)$$

where Y equals annual streamflow in inches from the treated watershed, and X equals annual streamflow in inches from the control. The correlation coefficient $R = 0.997$ is highly significant, and the standard error of estimate is 0.673 inch. The estimated annual increases, ΔY are

TABLE 3. Increases in annual streamflow with precipitation and time.

Year	Annual precipitation X_p	Time since treatment X_t	Estimated increase in streamflow ΔY
	Inches	*Years*	*Inches*
1949–50	92.94	1	3.96
1950–51	76.88	2	2.40
1951–52	87.01	3	2.61
1952–53	70.70	4	0.78
1953–54	79.55	5	1.45
1954–55	68.94	6	0.62
Average	79.34	3.5	1.97

shown in the last column of Table 3, together with annual precipitation, X_p and a time variable, X_t, reflecting year since initial cutting. The data suggest that a linear multiple regression exists with ΔY as a dependent variable and X_p and X_t as independent variables.

The derived multiple regression is:

$$\Delta Y = -3.330 + 0.0807X_p - 0.3150X_t \qquad (2)$$

The multiple correlation coefficient $R = 0.985$ is significant at the 1-percent level and the standard error of estimate is 0.287 inch. The regression coefficients of X_p and X_t are significant at the 5-percent level.

The expected increases in streamflow in column 3 of Table 4 are obtained from equation (2) by substituting observed values of precipitation and time from Table 3. These values can be compared with those in column 4 of Table 3 to obtain the deviations from the multiple regression line.

The partial regression coefficient for precipitation shows that a change of 10 inches in precipitation will produce 0.80 inch change in streamflow increase. The information at hand does not permit an explanation of this result in terms of the physical processes involved.

The partial regression coefficient for time shows a decrease of 0.31 inch for each year elapsed after treatment. A trend is revealed in column 4, Table 4, where the normal precipitation value of 80 inches has been substituted in equation (2). Since regrowth is occurring from the cut stumps (Fig. 4), it is logical to expect that treatment effect on streamflow will diminish with time and, in fact, at some future date will not be noticeable. The linear time relationship assumed for statistical analysis is arbitrary although it fits the limited data fairly well. Lengthening of the treatment period will better define the nature of the streamflow-time relation and might, for example, turn out to be a logarithmic curve. With the present data, extrapolation is not warranted.

Precipitation Minus Streamflow (P Minus RO)

The annual water balance for a watershed may be represented by the equation:

Precipitation = Evapotranspiration + Streamflow + Change in storage

where all quantities are expressed, for example, in inches of water. Losses to deep seepage are considered negligible. Storage includes all water in the soil reservoir. When summed over a number of years, the net change in storage will be small compared with the other quantities. At the Coweeta Hydrologic Laboratory the water year from May 1 to April 30 is used because the change in storage between the beginning and ending of this 12-month period is usually small, owing to winter and

TABLE 4. Estimated increases in streamflow from equation (2).

Year	Time since treatment	Estimated increases in streamflow: Observed precipitation[1] ΔY	Estimated increases in streamflow: Normal 80 inches precipitation ΔY
	Years	*Inches*	*Inches*
1949–50	1	3.86	2.81
1950–51	2	2.24	2.50
1951–52	3	2.75	2.18
1952–53	4	1.12	1.87
1953–54	5	1.51	1.55
1954–55	6	0.34	1.24
Average		1.97	2.02

[1]Data from Table 3.

spring rains that recharge the soil reservoir each year. Therefore, precipitation minus streamflow, P — RO, is approximately equal to evapotranspiration on an annual basis, and the average P—RO for 5 or 6 years may be considered equal to the true mean annual evapotranspiration. These values are shown in Table 5.

TABLE 5. Annual precipitation minus streamflow for the period May 1 to April 30.

Year	Control	Treated
	Inches	*Inches*
PRETREATMENT PERIOD		
1941–42	26.58	28.35
1942–43	29.51	32.49
1943–44	27.87	30.70
1944–45	29.14	30.58
1945–46	25.04	28.59
1946–47	26.47	27.83
1947–48	26.79	29.97
Average	27.34	29.79
TREATMENT PERIOD		
1949–50	19.47	19.80
1950–51	28.50	27.60
1951–52	25.48	25.67
1952–53	27.59	29.18
1953–54	33.01	33.68
1954–55	28.45	29.76
Average	27.08	27.62

The average annual evapotranspiration on the control watershed is 27.2 inches. Average annual evapotranspiration on the treated watershed before cutting was 29.8 inches with an adjusted average decrease of 1.9 inches following cutting. This change is significant at the 1-percent level, with confidence limits of 0.4 to 3.2 inches. This agrees closely with the streamflow regression analysis where the precipitation variable was not considered. This decrease amounts to 6 percent of the mean annual evapotranspiration.

Seasonal Streamflow

Annual streamflow and evapotranspiration do not tell the complete story because of seasonal interactions of many factors affecting the water balance. For example, on these experimental watersheds, soil moisture and ground water normally are depleted during the growing season while the reverse takes place during the dormant season. Minor variations in the over-all process occur from month to month. For this study the breakdown for growing and dormant seasons only will be considered.

Growing Season. Streamflow totals for the 6-month period from May 1 to October 31 are the basis for growing season regressions. Comparison of regression lines for the two periods by the analysis of covariance showed that the estimated mean

TABLE 6. Estimated increases in growing-season streamflow, with precipitation and time since treatment.

Year	Growing season precipitation[1] X_p	Time since treatment X_t	Estimated increases in streamflow From equation (3) ΔY	From equation (4) ΔY
	Inches	*Year*	*Inches*	*Inches*
1949	62.90	1	0.85	1.92
1950	45.81	2	1.48	1.55
1951	38.19	3	1.39	1.17
1952	27.90	4	0.45	0.80
1953	30.80	5	0.69	0.42
1954	29.34	6	0.02	0.04
1955	45.76	7	—0.38	—0.33
Average	40.10	4.0	0.64	0.80

[1]Includes April 1–October 31 precipitation, because April precipitation influences streamflow in subsequent months.

increase in streamflow for the 6-year treatment period amounts to 0.79 inch and is significant at the 1-percent level with confidence limits of 0.05 to 1.52 inches.

The estimates for individual years are obtained from the regression based on the 1942 to 1948 period, which is given by:

$$Y = -1.747 + 0.9945X \quad (3)$$

where Y equals growing-season streamflow in inches on the treated watershed, and X equals seasonal streamflow in inches on the control. The correlation coefficient is R = 0.9981, and the standard error of estimate is 0.216 inch.

The seasonal streamflow increases for each year were obtained from equation (3) and these are shown in column 4, Table 6, together with a precipitation and time variate. Data for the seventh (most recent) growing season have been included. The first year increase of 0.85 inch is considered an extreme value, as the estimated streamflow Y is widely extrapolated from equation (3). The estimate of streamflow for this year is obtained by substituting X = 35.11 inches in equation (3), which is actually based on a range of X from 12 to 23 inches in the pretreatment period. This value was omitted, therefore, and the multiple regression computed from the second to the seventh year data. The analysis shows the partial regression coefficient of X_t to be very highly significant, while that for X_p is not significant. This leads to the following estimate of ΔY for the treated watershed:

$$\Delta Y = 2.301 - 0.3763\ X_t \quad (4)$$

Correlation coefficient R is 0.9535, and the standard error of estimate is 0.288 inch.

The estimated increases in streamflow in column 5 of Table 6 are obtained from equation (4). The average increase for the first 6 years is 0.98 inch. This includes the estimate for the first year, which is extrapolated from equation (4). The effect of regrowth on streamflow is evident in column 5, Table 6; the regression analysis showed the time trend to be statistically significant. In contrast with the annual results, the increases in growing season streamflow are independent of the amount of precipitation.

Dormant Season. The dormant season regression, November 1 to April 30, for the 1941-1948 period is given by

$$Y = 1.848 + 0.8803\ X \quad (5)$$

where Y equals seasonal streamflow in inches on the treated watershed and X equals seasonal streamflow in inches on the control. The correlation coefficient R = 0.9985 is highly significant and the stand-

TABLE 7. Estimated increases in dormant-season streamflow, with precipitation and time since treatment.

Year	Dormant season precipitation[1] X_p	Time since treatment X_t	Estimated increases in streamflow From equation (5) ΔY	From equation (6) ΔY
	Inches	*Years*	*Inches*	*Inches*
1949–50	49.76	1	1.74	1.42
1950–51	40.08	2	0.40	0.58
1951–52	60.57	3	1.63	1.79
1952–53	49.49	4	0.62	0.86
1953–54	54.77	5	1.12	1.04
1954–55	47.30	6	0.54	0.36
Average	50.33	3.5	1.01	1.01

[1]October 1 to April 30.

ard error of estimate is 0.142 inch. The estimated average increase in streamflow for the treatment period as obtained by the covariance analysis is 1.00 inch, which is significant at the 1-percent limit with confidence limits of 0.28 to 1.72 inches.

Since October rainfall strongly influences subsequent seasonal streamflow, it has been included in the seasonal precipitation, that is, October 1 to April 30. The derived multiple regression, including a time and precipitation variable, is given by:

$$\Delta Y = -1.785 + 0.0679X_p - 0.1785\,X_t \qquad (6)$$

The multiple correlation coefficient $R = 0.918$ just fails to reach the 5-percent significance level, and the standard error of estimate is 0.259 inch. The partial regression coefficient of X_p is significant at the 5-percent level, and that of X_t is significant at the 10-percent level. X_t has been retained in the regression from logical considerations as mentioned earlier. The regression estimates are shown in column 5, Table 7.

It is quite likely that with additional data the time trend will be more clearly defined. Increases in streamflow for this season are apparently related to precipitation. The rate of change is 0.67 inch for 10 inches of precipitation, which compares with the annual figure of 0.80 inch per 10 inches of precipitation. This is not unexpected, since the annual streamflow values include the total for this season.

Hydrograph Analysis

Maximum flows during storm periods have not been changed by the cutting treatment. Annual streamflow is still controlled by ground water with no change in proportion of total streamflow contributed by stormflow or ground water.

Summary and Conclusions

The results to date illustrate that cutting a dense understory of laurel and rhododendron in hardwood stands decreased evapotranspiration and correspondingly increased streamflow in a perhumid climate in the Southern Appalachian Mountains where the understory covered about 80 percent of the area. It does not follow that similar effects would be obtained under a different climatic and soil condition.

Based on normal precipitation, the following results were obtained:

Cutting increased annual streamflow on the average 2.0 inches for the first 6 years after treatment. This means that average annual evapotranspiration correspondingly decreased 2.0 inches following

cutting. The average increase in annual streamflow is 4 percent, while the decrease in evapotranspiration was 6 percent.

During the first year after the watershed was cut, streamflow increased 2.8 inches. Observed gains in annual streamflow were proportional to the amount of precipitation, which is the basis for referring these results to normal precipitation. The increase declined with time, and by the end of the sixth year was down to 1.24 inches. The future behavior of streamflow on the treated watershed cannot be accurately predicted from the data at hand. Eventually, it appears that regrowth will restore the watershed very closely to its former vegetative condition and the effect of treatment on streamflow will disappear.

The average increase for the dormant season amounted to 1.0 inch, and for the growing season about the same. Observed dormant season gains in streamflow appear proportional to total precipitation. In contrast, the increase during the growing season seems to be independent of precipitation for the observed range. Growing and dormant season gains also declined with time. The reason for this was that cut vegetation was allowed to sprout, and the mountain hardwood overstory continued growing.

Where objectives of watershed management favor increases in streamflow through special cutting of forest vegetation, there is evidence that treating understory vegetation alone provides worthwhile gains.

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Balsam Fir Tree Volume In The Lake States

BY
D. O. PRIELIPP

DURING the summer of 1951, an intensive study of rot in balsam fir was conducted in the Upper Peninsula of Michigan. In connection with the study, the volumes of 476 trees were determined. These data provided information: (1) on the effect of site as defined by soil moisture classes on tree volume; (2) on the relative effectiveness of two recently-developed methods of volume table construction; and (3) from which new balsam fir volume tables could be constructed.

Methods

Eight balsam fir stands scattered throughout the Upper Peninsula of Michigan were sampled and classified as to their soil moisture condition by the following criteria:

Swamp. Low, level areas in which the soil is wet, spongy, and well-saturated the year around. The sample included 118 trees from 3 stands in this site category.

Transition. Fairly low, gently-sloping land which terminates in a swamp. The surface is dry the year around except for possible spring flooding. The water table is 1 to 5 feet below ground level. A total of 288 trees from 3 stands in this grouping were measured.

Upland. High land, where the water table is 6 feet or more below the ground surface. Included are the tops of ridges and high, level plains. In the two upland stands sampled, the ground levels were more than 10 feet above the first free ground water. The number of trees studied in this category was 70.

As the survey was in conjunction with pulpwood cutting operations, stem measurements were taken at 100-inch intervals. The stem diameters outside and inside bark were taken at the stump and at each 100-inch interval up the bole until a 3-inch top diameter outside bark was reached. The height of the stump and length of the top were also recorded.

In the office, the eight stands were separated according to their occurrence on upland, transition or swamp sites. The volume of each tree was calculated graphically on arithmetic graph paper (Spurr, 1952, pp. 47-50). For each site two volume curves were drawn, one by the combined-variable graphic method (*op. cit.* pp. 111-116) and the other by the revised harmonized-curve method (*op. cit.* p. 120). The former was recommended as the best short-cut method, and the latter as the best comprehensive graphical technique for the construction of cubic-volume tables.

To determine the volume differences of trees growing on different sites, volume tables constructed by the combined-variable method were used. In this method the diameter at breast height (DBH) is squared and then multiplied by tree height

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The author is Forest Pathologist for Kimberly-Clark of Michigan, Inc. The investigation was financed by a fellowship grant from the Kimberly-Clark Paper Corporation and carried out at the School of Forestry, University of Minnesota under the supervision of Professor Stephen H. Spurr.

to give a "combined-variable" value that is a direct function of volume. The data are then sorted into classes according to this combined variable (D^2H). The mean volume of each class is then plotted over its corresponding D^2H. A smooth curve is then drawn through the averages of these points. From this smooth curve the volumes of trees of known DBH and height can be determined. A standard volume table may thus be constructed from a single volume-D^2H curve. The preliminary volume tables were constructed for total cubic-foot volume inside bark.

The swamp, transition, and upland curves were plotted on a single graph to facilitate comparison (Figure 1). Very little difference was found in the volumes of small trees (D^2H of 4000 or less, approximately equivalent to an 8-inch 60-foot tree) irrespective of soil moisture condition. For large trees, there is no significant difference between upland and transition tree volumes, but the swamp stands have about 10 percent more volume per tree above the 6000 D^2H class (Table 1).[1]

Although the plotting of volume over D^2H showed that swamp trees had more volume per tree in the higher D^2H classes, it did not show why. Therefore, the two variables—DBH and height—were plotted against each other for each of the three sites (Figure 2). The height-diameter relationships for swamp and transition trees as shown by these curves are quite similar, with transitition trees having a slight height advantage for a given DBH class. The upland curve, though, shows a marked difference in both value and trend. On these sites, the height for a given DBH class is consistently lower. Height also levels off at a much lower diameter than on the other two sites.

With the use of the height-DBH and the volume-D^2H curves a local volume table was constructed for each type (Table 2). In comparing these values, the swamp volumes are used as a basis (100 percent). A comparison of swamp and transition tree volumes shows a higher volume in the small-diameter transition trees due to the slightly greater heights on that site. As DBH increases, the effect of the greater height of transition trees is offset by the better form of the swamp trees. Above the 10-inch DBH class, transition tree volumes are about 10 percent less than those of swamp trees.

The comparison of upland and swamp tree volumes reveals no appreciable difference in the smaller size classes. As diameter increases, however, there is a widening gap between the volumes of upland and swamp trees of the same diameter class. The upland trees have 30 percent less vol-

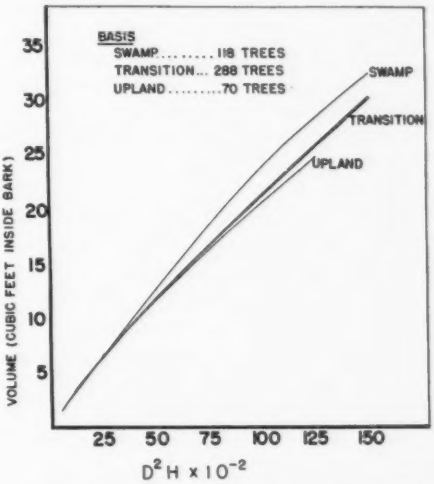

FIGURE 1. *Combined-variable volume solution for balsam fir for three sites in the Upper Peninsula of Michigan.*

[1]Following a suggestion of a reviewer, 17 additional trees over 10 inches DBH were measured from swamp sites. The data from these did not appreciably change the volume curve for swamp trees when they were included.

TABLE 1. Comparison of the volume of trees of similar dimensions on different sites in the Upper Peninsula of Michigan.

	Swamp		Transition		Upland	
D^2H	Volume	Percent	Volume	Percent	Volume	Percent
			Volume in Cubic Feet			
2000	5.3	100	5.4	102	5.4	102
4000	10.1	100	9.7	96	9.8	97
6000	15.0	100	13.4	89	13.6	91
8000	19.8	100	17.2	87	17.2	87
10000	23.7	100	21.0	89	20.5	86
12000	27.3	100	24.7	90	24.0	88
14000	30.7	100	28.5	93	27.4	89
16000	34.3	100	32.2	94	30.4	89

ume at 14-inches DBH. This lower volume of upland trees is due to their having more taper and less height for a given DBH class than the swamp trees.

Transition and upland trees, even though they have about the same volume per D^2H class, have a different distribution of volume within the tree. The transition trees are tall and highly tapered as is evidenced by their greater height and lower volume per DBH class than swamp trees. Upland trees are shorter with still greater taper.

The new volume solutions may be compared with two previously constructed volume tables: (1) Spurr's volume curve (1952), based on 250 trees gathered from New York, New England and Minnesota: and (2) the balsam fir volume table by Lotti and Gevorkiantz (Brown and Gevorkiantz, 1934, Table 23) based on 60 Wisconsin trees.

Spurr's solution proved to be intermediate between the transition and swamp curves. This is to be expected because it was constructed from about an equal number of upland, transition, and swamp trees. The curve drawn from the Lotti-Gevorkiantz solution was lower than all the other curves, but most closely approximated the upland curve. According to Gevorkiantz (personal communication), the trees from which this curve was developed were open-grown, and would be expected to have less volume than comparable forest-grown trees.

In conclusion, several differences in tree form and volume are attributable to site, as defined by soil moisture relationships. Transition trees attain the greatest heights for a given DBH class. Swamp trees are the best formed. A difference in form exists between transition and upland trees even though they have the same volume for a given D^2H class. The transition trees are tall and thin while the upland trees are short and stocky. The construction of a local volume table for each site showed that, in the low DBH classes, the greater height of the transition trees gave them more volume than the better formed swamp trees. In the higher DBH classes, however, the better form of the swamp trees more than compensated for their slightly lower height.

In comparing the new volume table solutions for swamp and dry sites against previously-constructed volume tables, it appeared that a new balsam fir volume table was needed.

Comparison of Two Methods of Volume Table Construction

In *Forest Inventory*, Spurr recommends two methods of volume table construction: (1) the combined-variable method where speed and simplicity are desired; and (2) the revised harmonized curve method where high precision is wanted. Volume

TABLE 2. Local cubic-foot volume tables for balsam fir growing on different sites in the Upper Peninsula of Michigan.

	Swamp			Transition			Upland		
DBH	Height	Volume	Percent	Height	Volume	Percent	Height	Volume	Percent
6	41	3.9	100	44	4.2	107	40	4.0	102
7	46	5.8	100	48	6.2	107	43	5.8	100
8	50	8.1	100	51	8.4	104	46	7.6	94
9	53	10.9	100	54	10.6	97	48	9.7	89
10	56	14.2	100	58	13.1	92	49	11.6	82
11	60	18.1	100	61	16.0	88	50	13.9	77
12	63	21.9	100	64	19.6	89	51	16.1	74
13	66	25.8	100	67	23.5	91	52	18.4	71
14	69	29.8	100	70	28.0	94	52	21.0	70

curves were made by both methods for each of the sites and for all the data grouped together. Combining all the trees into a single table was done to find out how much precision is lost by use of a composite table.

Comparisons were based upon standard statistical tests: (1) *average deviation,* the arithmetic sum (ignoring plus and minus signs) of all the deviations of the actual volumes from the smoothed volume curve, divided by the number of trees: (2) *aggregate deviation,* the algebraic sum of the deviations of actual from curve volumes divided by the number of trees: (3) *standard error of estimate:* and (4) the *coefficient of variation,* or the standard error of estimate expressed as a percent of the average tree volume. These data are set forth in Table 3.

Only about half the time is needed to construct a volume table by the combined-

TABLE 3. Comparison of the statistical tests of the two methods of volume table construction: (1) The combined-variable method, and (2) the revised harmonized curve method.

Data Group	Basis Number of trees	Average deviation	Aggregate deviation	Standard error of estimate	Coefficient of variation
			Cubic Feet		*Percent*
Upland					
Comb.-Var.	70	0.65	+0.04	0.89	10
Rev. Harm.	70	Not possible—sample too small			
Transition					
Comb.-Var.	288	.59	— .01	.84	10
Rev. Harm.	285	.56	— .004	.77	9.5
Swamp					
Comb.-Var.	118	.55	— .03	.70	8
Rev. Harm.	118	.52	— .02	.79	9
Composite					
Comb.-Var.	473	.62	— .06	.87	10.3
Rev. Harm.	473	.59	+ .04	.88	10.4

variable graphic method as is required by the revised harmonized-curve method once the field work and volume computations are made and recorded on index cards. The procedure of the combined-variable method is easier to comprehend and requires less mathematical knowledge. Nevertheless, a comparison of the standard errors of estimate and coefficients of variation for each method shows that the combined-variable method yields results that are as good as those given by the revised harmonized-curve method.

The combined-variable method is better suited to small groups of data than is the revised harmonized-curve method. For example, the upland site was represented by only 70 trees, but the statistical tests showed good results by the former method. This amount of data, however, was insufficient for the latter method. When a great range in height exists the data must be split up into such small groups (when using the harmonized-curve method) that a line cannot be drawn accurately through the points.

When a large amount of data is available, the harmonized-curve method has been thought preferable. A comparison of the statistical tests for the composite table (473 trees), though, shows that the two methods yield comparable results. While it is true that the average and aggregate deviations are slightly smaller by the revised harmonized-curve technique, the improvement is too small to justify the more complicated method. In this instance at least, the simpler combined-variable method is preferable. It is fast, easy, and readily understandable, and may be effectively used when only a few tree measurements are available. It yields nearly as good results as the more tedious method. Moreover, since the whole volume-relationship is reduced to a single regression line, curvilinearity in this relationship may be readily checked and taken into account. Actually, the lower ends of the regressions in Figures 1 and 3 were found to be curvilinear in all

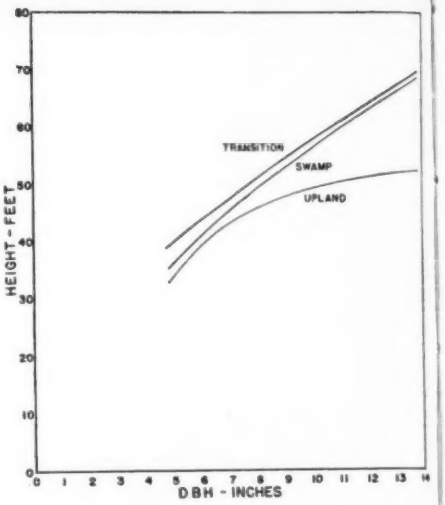

FIGURE 2. *Height-diameter curves for balsam fir on three sites in the Upper Pensinula of Michigan.*

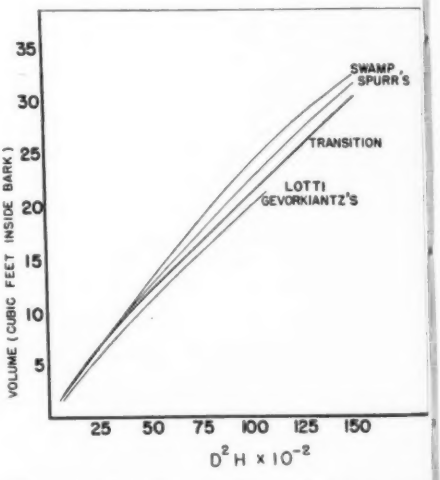

FIGURE 3. *Comparison of new combined-variable solutions with: (1) Spurr's combined-variable solution for balsam fir in the Northeast and Lake States; and (2) combined-variable solution derived from the Lotti-Gevorkiantz volume table.*

TABLE 4. Second-growth balsam fir volume table. Total bole volume inside bark. Constructed by the combined-variable method.

DBH	Site	Total height in feet 30	40	50	60	70
		Volume in cubic feet				
4	All	1.0	1.6			
5	All	1.9	2.6	3.3		
6	All	2.8	3.8	4.7		
7	All	3.9	5.1	6.3	7.4	
8	All	5.0	6.6	8.0	9.4	
9	Dry sites					
	Wet sites		8.1	9.9	11.6	
10	Dry sites				13.5	15.3
	Wet sites		9.8	11.9	15.1	17.1
11	Dry sites			13.6	15.8	18.0
	Wet sites			15.2	17.6	20.0
12	Dry sites			15.7	18.4	21.0
	Wet sites			17.4	20.3	23.2
13	Dry sites			18.0	21.1	24.1
	Wet sites			20.0	23.2	26.5
14	Dry sites				24.0	27.7
	Wet sites				26.4	30.2

Based on 472 trees.

TABLE 5. Second-growth balsam fir volume table. Merchantable volume inside bark to 3-inch top outside bark. Constructed by the combined-variable method.

DBH	Site	Total height in feet 30	40	50	60	70
		Volume in cubic feet				
4	All	.8	1.4			
5	All	1.7	2.4	3.2		
6	All	2.7	3.6	4.5		
7	All	3.7	4.9	6.0	7.1	
8	All	4.8	6.3	7.6	8.9	
9	Dry sites					
	Wet sites		7.7	9.3	10.9	
10	Dry sites				12.5	14.2
	Wet sites		9.2	11.2	14.2	16.1
11	Dry sites			12.6	14.4	16.6
	Wet sites			14.3	16.4	18.7
12	Dry sites			14.5	16.9	19.2
	Wet sites			16.4	19.1	21.7
13	Dry sites			16.6	19.4	22.2
	Wet sites			18.7	21.8	25.0
14	Dry sites				22.0	25.3
	Wet sites				24.8	28.4

Based on 472 trees.

instances. The revised harmonized-curve method also yields good results, but is more time consuming and is not as versatile as the other. It is particularly suited for the handling of large numbers of tree measurements (1000 or more).

The question may here be raised as to whether a composite volume table for balsam fir should be used, or whether separate volume tables for each site are necessary. The coefficients of variation of the individual site solutions compared to that of the composite table indicate a 1-percent decrease in precision for the combined table. This is true for both methods of construction. The greater convenience of a single table would easily offset the 1-percent decrease in accuracy, if the deviation were consistent throughout the regression. It has already been shown, though, that the variation in volume on the different sites is pronounced in the large trees. A composite volume table for balsam fir is therefore justified only for trees up through 9-inches DBH. For 10 inch and larger trees, two volume solutions are needed: one for swamp trees, and one for upland and transitions trees combined.

The only published cubic-foot volume table for balsam fir in the Lake States is that of Lotti - Gevorkiantz. Gevorkiantz (personal communication 1952) pointed out that the trees used in constructing this table were open-grown and; therefore, would naturally have a lower volume for a given diameter-height class than corresponding forest-grown trees.

This investigation indicates that there is a significant difference in the volume of large trees growing on different soil moisture conditions. A separation of trees by soil moisture site classes shows about a 10-percent higher volume for a given diameter and height (10-inches DBH and over) for swamp trees than for corresponding transition and upland stems. These two facts:

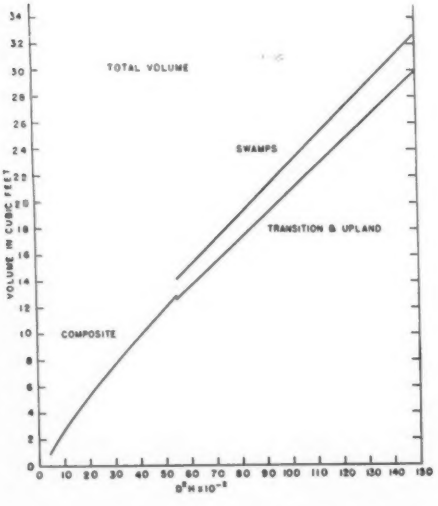

FIGURE 4. *Final composite combined-variable volume solutions for balsam fir in the Upper Peninsula of Michigan. Total cubic-foot volume inside bark.*

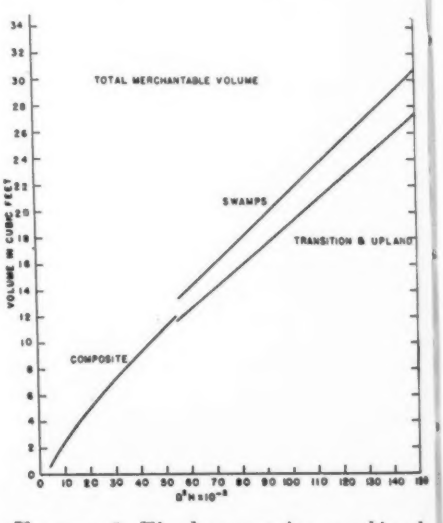

FIGURE 5. *Final composite combined-variable volume solutions for balsam fir in the Upper Peninsula of Michigan. Merchantable cubic-foot volume inside bark above a 1-foot stump to a 3-inch top outside bark.*

(1) lack of a good balsam fir volume table, and (2) the form differences of trees growing on different moisture conditions —make the construction of new volume tables desirable.

The two tables presented were constructed by the combined-variable graphic method and are based on the entire 476 trees. For the higher diameter classes, volumes are given separately for trees growing on wet and dry sites. The volume solutions are presented in both graphical and tabular form. Table 4 and Figure 4 give total cubic-foot volume inside bark including stump and top. Table 5 and Figure 5 present merchantable cubic-foot volume inside bark above a 1-foot stump to a 3-inch top outside bark.

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Water: Yearbook of Agriculture, 1955

Edited by Alfred Stefferud, 751 pp., illus. Supt. of Documents, Washington, D. C. 1955. $2.00.

Review by Robert E. Dils.
School of Natural Resources, University of Michigan

WATER, the 1955 Yearbook of Agriculture, faces and satisfies a very unusual challenge. Its 751 pages are packed with facts, with technical information, and with data emerging from current research. Thus the book becomes a valuable reference source for farmers, foresters, land managers, hydrologists and ecologists. The unusual challenge presented to the writers and editors of this volume is found in the fact that it also had to be planned to interest many hundreds of people not technically or scientifically trained — the average American who wants further information on some specific question dealing with our water resource—the average American who is realizing more and more that this resource could be depleted and should be conserved and managed now to prevent such depletion.

To explain in one volume the nature, behavior, and conservation of water in agricul-

ture is in itself a formidable assignment. To have succeeded in presenting such a wealth of material with technical accuracy yet is an interesting and readable style is indeed a tribute to the editors and authors.

The book is conveniently divided into sections which deal with each major facet of the subject. Our water needs, sources of supply, use of water for irrigation, water for forests, water and our crops, are among the major headings discussed. In the initial article, "The Story of Water as the Story of Man," Bernard Frank gives a most interesting historical account of water needs and uses and sets a fast pace for subsequent discussions. "From Ocean to Sky to Land to Ocean" by William C. Ackerman, E. A. Colman, and Harold O. Ogrosky should be required reading for all students and practitioners in agriculture and the natural sciences.

E. G. Dunford and Sidney Weitzman present a fact-packed story on managing our forest watersheds for erosion control which offers guides to the forester for reducing erosion occasioned by roads, logging, fire, and grazing. Of particular interest to the western forester is the description by B. C. Goodell and H. G. Wilm on how to get more snow water from forest lands. Of special importance to both foresters and ecologists are the articles by G. S. Hayes and Jesse H. Buell telling of the need and use of water by trees, and that by C. Allan Friedrich describing fire on the watersheds of the nation.

Foresters and land managers will find specific information on the management of water on western range lands, drainage and forest management in the South, water and recreational land use, and several articles treating with the management of watersheds to provide better fishing and better wildlife habitats. Of general interest are discussions ranging from flood control, ground water, and weather cycles through home gardening to lawn care. As interesting sidelights there are also articles on rain-making, possible conversion of salt water, and the use of divining rods. The Yearbook offers sixteen pages of descriptive photographs and over 150 illustrations and charts.

A fitting conclusion to the Yearbook is a look to the future in which the reader is apprised of the problems we face in water legislation and financing, and is given a picture of what the U. S. Department of Agriculture is doing and plans to do in further research.

The very size and scope of the book will probably be the cause of the few negative comments which may be received. Groups or individuals interested in one specific phase may wish that there were more articles on that phase, while another group may wonder why certain problems and projects were not discussed at all. Possibly one weakness from the lay reader's standpoint might be mentioned. In certain discussions the nature of the subject matter virtually dictates technical terminology, particularly in reference to the measurement of water in the various water units. A simplified discussion of how and in what units water is commonly measured would have been valuable.

The saying that "water is everyone's business" is borne out in this volume, not only in the range of subject matter but also in the list of authors who have contributed to it. In compiling the Yearbook, the department has called upon engineers, geologists, climatologists, and pollution experts as well as foresters, soil scientists, agronomists, and many other specialists—both within and outside the Department of Agriculture.

The timely appearance of the Yearbook in 1955 indicates an increasing awareness of the significance of land management in the handling of our water resource. "We cannot live without water," states Mr. Stefferud in his preface. "We could live better if we knew more about it." Every land manager must assume responsibility for the management of the water resource on the lands under his administration whether he be a farmer, a forester, or a refuge manager. The 1955 Yearbook provides an excellent tool and furnishes many useful guides to meet this objective. Certainly every forester should acquire and use this valauble tool and reference.

Needle Oils of Three Pine Species and Species Hybrids

BY
ROBERT Z. CALLAHAM

THE COMPOSITION and characteristics of the needle oils of western pines may provide criteria for distinguishing pine hybrids and may help explain why some needle-feeding insects select certain pine species as hosts.

Many insects feed on the foliage of pines during some part of their life cycle. One such insect is the pine reproduction weevil (*Cylindrocopturus eatoni* Buch.). This weevil is particularly destructive to seedling pines in California plantations and forests (Eaton, 1942), but the pine species differ in susceptibility. Ponderosa pine (*Pinus ponderosa* Laws.) and Jeffrey pine (*P. jeffreyi* Grev. and Balf.) are particularly susceptible to attack. Coulter pine (*P. coulteri* D. Don) is immune. Miller (1950) demonstrated that the Jeffrey-Coulter interspecific hybrid possesses some of the resistance of its Coulter parent.

Because the weevils have to feed on pine foliage before they attack the stem,[1] the hypothesis was developed that selection of susceptible hosts by the weevils is related to the needle-feeding habit. As one step in testing the hypothesis, the volatile oils contained in the needles of three pine species and three hybrids were investigated to determine whether qualitative differences between host species might be one factor influencing such selection. The species and hybrids studied were ponderosa, Jeffrey, and Coulter pines, the F_1 Jeffrey-ponderosa hybrid, the backcross of a natural Jeffrey-Coulter hybrid to Jeffrey, and the wind-pollinated progeny of the same natural hybrid.

Few articles dealing with the yield and composition of pine-needle oils have been published. This literature is reviewed adequately by Bailey (1948), who studied interspecific differences in yield of oil. Schorger (1919) showed that the yield of needle oil is dependent upon the number and size of the resin canals in the needles of each species. Bailey showed that yield also was affected by time of harvesting needles, age of the trees, and the prevailing growth conditions. Schorger contributed most to knowledge of the composition of the oils. He and a few others reported that the needle oil of each pine species has a characteristic chemical composition, each differing in the amounts of terpenes, sesquiterpenes, and terpene alcohols and their

[1]The late J. M. Miller, Entomologist, Berkeley Forest Insect Laboratory, showed that foliage feeding by the adult is obligatory.

The author is a Research Forester at the California Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture. The study was guided by Dr. A. B. Anderson, Forest Products Laboratory, University of California, and Dr. N. T. Mirov, Institute of Forest Genetics.

esters present. Of the terpenes, alpha- and beta-pinene occur most frequently. The pleasant odors of the oils are due primarily to borneol and bornyl esters.

Of the three pine species included in this particular study, only ponderosa pine had been studied previously. Schorger found that the physical properties of 10 samples of ponderosa pine leaf oil were: Specific gravity (d^{15}_4°), 0.8718 to 0.8849; specific rotation (D_{22}°), −15.73° to 19.59°; index of refraction (D_{15}), 1.4789 to 1.4815.

Procedure

Needle collection. Needles were collected at the Institute of Forest Genetics, Placerville, California, in February and early April, 1951. According to Bailey, the largest accumulation of volatile oils in the needles occurs during these spring months. Only the most recent (1950) twigs with the attached needles were collected. All twigs were taken from the lowest branches so as not to deform the young trees. The trees were from 9 to 22 years of age. Foliage was taken from several trees of each species or hybrid.

The twigs from different trees varied considerably in their rate of growth, but the effect of this factor on the qualitative or quantitative variation in needle oils is unknown. As twigs were removed from the trees, they were placed in heavy canvas bags. Then the bags of foliage were stored at 0°C. pending distillation. Some were stored as long as 4 weeks. Bailey's work indicates that 4-week storage at low temperature does not cause any significant change in either the yield or characteristics of the needle oils.

The bags of foliage were removed from cold storage and the needles were stripped from the twigs. Stripping was greatly facilitated by having frozen needles. As the needles warmed to room temperature it become more difficult to pull them from the twigs without removing large strips of phloem and cortex. To avoid any contamination of the volatile needle oil by the turpentine from the stem, special care was taken to prevent including stem tissues with the needles. An example of such contamination was reported by Schorger.

Oil distillation. The needles were chopped into short segments just before distillation. The objective of this treatment was to expose the resin ducts and thus to facilitate extraction of the volatile oil. A small sample of the chopped needles was reserved for a moisture determination. The remaining needles (4,000 to 6,000 grams per species) were weighed before being placed in the still.

The still was made from a 5-gallon can with a friction lid. The can was fitted with a pressure release, condenser, and screen, which was placed near the bottom to prevent submerging the needles in the boiling water. The distillate passed from the can through a glass "L" sealed in the lid and thence through a straight water-cooled glass condenser into a flask immersed in an ice bath. A small amount of boiling water was poured over the needles; then the still was sealed quickly. Most of the oil (90 to 95 percent) was collected in the first 30 to 40 minutes of distillation. However, the distillations were continued until there were no droplets of oil in a 10 to 15 cc. sample of distillate. This usually required 3 to 4 hours. The oil was separated from the water in a separatory funnel and was placed in a small vial. A few crystals of anhydrous sodium sulfate were added to remove the water from the oil. The vials were sealed and refrigerated at 5° C. for at least 24 hours.

Oil analysis. The percent yield, both on a dry- and on a wet-weight basis, was determined. Then measurements were made of the following physical properties of the oil: Specific rotation, index of refraction, and specific gravity.

Results

The data (Table 1) show no striking interspecific differences in physical properties of the needle oils analyzed for this study. Most properties of the ponderosa pine

TABLE 1. Physical properties and yield of needle oil from pine species and species hybrids.

Pine species or hybrid	Specific gravity $d_4^{23°}$	Specific rotation $[\alpha]_D^{23°}$	Index of refraction $n_D^{21.5°}$	Yield		Date of Collection
				Wet wt.	Dry wt.	
				Percent	*Percent*	
Ponderosa	0.8814	—17°25′	1.4846	0.23	0.46	2/23/51
Jeffrey-ponderosa	0.8803	—13°55′	1.4842	0.29	0.56	4/ 3/51
Jeffrey	0.8707	—25°05′	1.4762	0.13	0.27	2/23/51
Jeffrey × natural Jeffrey-Coulter	0.8600	—23°45′	1.4741	0.15	0.32	2/23/51
Natural Jeffrey-Coulter × wind	0.8666	—29°00′	1.4830	0.19	0.41	2/23/51
Coulter	0.8744	—25°40′	1.4851	----	----	2/23/51

needle oil were close to the ranges given by Schorger. However, the index of refraction was somewhat higher than the value given by Schorger.

About 6 grams of Jeffrey pine oil were subjected to a crude fractional distillation. The object was to determine whether the needle oil of this species contained the large quantities of n-heptane present in Jeffrey pine oleoresin (Schorger). The physical properties of the needle oils from Jeffrey pine and the Jeffrey pine hybrids indicate that no large quantity of n-heptane was present. Furthermore, the results of the fractional distillation (Table 2) showed no discernible n-heptane (boiling point 98.4° C.) in the needle oil of this species. Since n-heptane is highly volatile, however, any small amounts which might have been present in the distillate could have been lost through evaporation during the steam distillation. There was not a sufficient amount of distillate in any of the fractions for determinations of the compounds present.

Discussion

The results of this investigation, which was limited to only a few trees of each species, do not indicate any striking interspecific differences in the physical properties of the needle oils. This does not preclude the possibility that the constituents of the turpentines differ. Further study of these constituents may determine whether needle oils are important in influencing the selection of host species by adult pine reproduction weevils.

The physical properties of the needle oil of the Jeffrey-ponderosa hybrid are intermediate between those of the parental species, as one might expect for F_1 hybrids. On the other hand, most properties of the Jeffrey-Coulter hybrids transgress the parental values. Logically, for a character controlled by many genes, one might expect to find such transgressive variation in the progenies of hybrids. The lack of interspecific differences in needle oils and

TABLE 2. Fractional distillation of the needle oil of Jeffrey pine.

Fraction number	Boiling point range	Yield
	°C.	*Percent*
1	0-150	0
2	150-160	32
3	160-170	35
4	170-200	12
5	200-240	11
6	Green oil	10
Total	----------	100

TABLE 3. Physical properties of oleoresin turpentine[1] and of needle oil from Jeffrey and Coulter pines and Jeffrey-Coulter hybrids.

Pine	Index of refraction		Specific rotation		Specific gravity	
	Turpentine	Needle	Turpentine	Needle	Turpentine	Needle
Jeffrey	1.3957	1.4762	— 1°	—25°	0.697	0.871
PJ × (PJ × PC)	1.4155	1.4741	— 6°	—24°	.732	.860
(PJ × PC) × (Wind)	1.4319	1.4830	— 9°	—29°	.767	.867
Coulter	1.4711	1.4851	—18°	—26°	.839	.874

[1]Turpentine properties determined by Zobel (1951).

the transgressive variation in the hybrids suggest that needle oils would not provide discriminating characters for studies of hybridization between these pine species.

It is possible to compare the needle oils from the Jeffrey-Coulter hybrids with the oleoresin turpentine from the same trees. Zobel (1951, 1951a) tapped the same hybrid trees and many Jeffrey and Coulter pines throughout California. The obvious specific differences and hybrid intermediacy shown by Zobel's data are not found in the needle oil data (Table 3).

From his work, Zobel concluded that Coulter pine could have been the pollen parent of the natural Jeffrey-Coulter hybrid. This conclusion would be substantiated by the index of refraction of the needle oils, but not by the values of specific gravity. The parentage of the hybrid could not be decided from the needle oil data.

Normal-heptane apparently is absent from the needle oil of Jeffrey pine, although it is present in the oleoresin turpentine (Mirov, 1954). A similar situation was found by Schorger in Digger pine (*P. sabiniana* Dougl.). The turpentines both of Jeffrey and of Digger pines have been reported as composed of 95 percent n-heptane. The apparent absence of n-heptane from the needle oils of both of these species adds further evidence in support of the statement by Schorger (1919, p. 733): "The phytochemical processes occurring in the wood and in the needles are . . . entirely different."

Summary

The physical properties of needle oils from three pine species and three species hybrids were analyzed to determine whether there were any major differences in oil composition between pines resistant and susceptible to the pine reproduction weevil. No striking differences between species were found. Further study of turpentine constituents is needed to determine whether differences in needle oils influence host selection by adult weevils. The properties of the needle oils of an F_1 pine hybrid were found to be intermediate between those of the parents. In the progenies of another hybrid some properties transgressed the parental values. The properties of needle oils do not appear to be as useful in studying pine hybridization as are the oleoresin turpentines. Normal-heptane, a major constituent of Jeffrey pine turpentine, was not found in a crude fractional distillation of Jeffrey pine needle oil.

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Tree-Ring Analyses of Danish Forest Trees

Arringsanalyser af Danske Skovtraer. By Erik Holmsgaard. Kandrup & Wunsch's Bogtrykkeri, 246 pp. Copenhagen. 1955. Reprints from "Det forstlige Forsgsvaesen i Danmark, Vol. XXII, Springforb:.

Review by Ake Wiksten
Weyerhaeuser Timber Company, Forestry Research Center, Centralia, Wash.

Foresters concerned with interpreting variations in width of annual rings will find this 246-page doctorate dissertation by Erik Holmsgaard of pointed interest. The text is in Danish with the customary English translation of the summary and the headings of numerous tables and figures. American foresters will find its utility further enhanced by the coverage given to famiilar or kindred species of trees. This extends from major emphasis on European beech (*Fagus silvatica*) and Norway spruce (*Picea abies*) — the most commonly planted of our introduced species, to include our own Douglas fir, Sitka spruce and the shrubby common juniper; the familiar introduced Scotch pine (*Pinus silvestris*) and also English oak (*Quercus robur*), European ash (*Fraxinus excelsior*), European alder (*Alnus glutinosa*) and silver fir (*Abies alba*). The author has undertaken to analyze the causes of year-to-year fluctuations in radial growth based on measurement of 78,000 rings of increment cores taken chiefly at diameter breast height. The cores were collected from representative trees in some 130 even-aged stands under intensive management—with thinning intervals of 2 to 8 years—distributed throughout Denmark.

The author's review of previous work dates back to observations by Leonardo 400 years ago, Linnaeus 200 years later, and the first comprehensive study by Reventlow about 1800. The consensus of findings from more recent investigations is that different species in common show marked variations in width of annual ring that can be explained readily where mainly one factor is limiting to growth. Thus, the main factor determining variation in growth is temperature in northern Scandinavian countries, whereas it is precipitation in Central Europe (the mountains excepted).

For the present study, the author determined the adequacy of sampling at 4 to 8 trees per stand. Each of nine districts in

Denmark was sampled by 6 to 24 stands for each species, except in the case of Douglas fir and Sitka spruce where only two stands were used. Sampling at six different heights was method used in one Norway spruce and two beech stands. In Norway spruce, the variation in ring width proved fairly uniform through all heights. For this species, sampling at D.B.H. should give a satisfactory estimate of growth. In the case of beech, the climatically conditioned variations in radial increment proved best sampled at a point two-tenths of the height above D.B.H. Thinning effects were less than variations due to climatic conditions. They amounted to an increase of 6 to 12 percent in radial increment, with development of the widest ring one to two years after treatment. In older stands this response to thinning is delayed; this coincides with the slower rate of crown closure in older stands. Fruiting proved to have a marked influence on growth. In the case of beech 130 years old, this amounted to a depression to 50 percent of the growth in years of no fruit production. For Norway spruce the reduction due to seed years was 25 to 35 percent of the radial growth. The influence of seed years increases with age of the stand; hence the influence of age alone could not be isolated. Different provenances showed only slight discrepancies in the variation of width of annual rings. Trees on good sites showed less fluctuation in growth than trees on poor site. Wind exposure effect was also studied by comparing trees subject to extreme exposure with trees in wind-protected stands. It was concluded that wind could cause significant depression in radial growth. In a discussion of an annual ring index as a correction factor for growth studies, it is recommended that the index be used when comparing growth for different periods of short duration in connection with stem analyses procedures in sample plots.

Erik Holmsgaard's contribution from his research culminates in the section on climatic conditioning of the variation in width of tree rings. The major climatic data employed were monthly precipitation and mean temperature in five localities in Denmark for the years 1900 to 1949. His analyses identified climatic indices that were correlated significantly with variations in growth of the ten species of trees. The five indices, in addition to climatic effects of the year before, were: precipitation from May to July, and in the winter; and, temperature from January to April, from June to September, and in the autumn of the year before. Each species showed significant correlation with a different combination of these indices. Grouping of the five indices shows that both precipitation and temperature were critical for oak, ash, alder, silver fir and Douglas fir; precipitation alone for beech, Norway spruce, Sitka spruce, and juniper; and temperature alone for Scotch pine.

Long-time variations of the climatic conditions have been studied for beech. Fluctuations with peaks in 1870 to 1879 and 1930 to 1939, and depressions in 1850 to 1859, 1910 to 1919, and in the 1940's have been observed. The periods show for beech considerable growth differences between the peak periods and the depression periods (25 percent). The long-time changes of growth coincide well wth the changes in the May to July rainfall.

In conclusion, Erik Holmsgaard's comprehensive analysis of tree-ring data for Danish conditions represents a significant advance in the knowledge on tree-rings that should find wide use by foresters.

Specific Gravity Estimations of Mature Loblolly Pine from Juvenile Wood and Seedling Limb Sections

BY
BRUCE ZOBEL
ROBERT RHODES

AN URGENT NEED in forest genetics research is to establish criteria whereby specific characters of the mature tree will be predictable from "juvenile" characters of a seedling or young tree. This need is especially urgent in the case of wood characters. In such studies, no results of breeding programs can ordinarily be assessed until the progeny under test have produced mature wood. Such diagnostic "juvenile" characters are rather rare. For example, Richens (1945) quotes Strohmeyer as indicating

> "The need of being able to select young pines in order that breeding projects may be expedited. Since, however, these do not give any direct information on the economic value of the adult trees, it is necessary to search for and establish correlations between morphological and physiological economic characters in the adults. This objective has not so far been realized. . . ."

Richens further states that

> "Characters such as vegetative vigor and wood quality cannot be directly estimated from seedlings."

Since 1945 several research projects have been initiated by various research workers in an attempt to correlate juvenile and adult characters in pines. Squillace and Bingham (1954) in their studies on blister rust of white pine have found some interesting parent-progeny relations in growth rate and form, while Larsen (1947) has been interested in the problem of correlation of juvenile and mature characters. Richens (1945) lists several projects underway and Mergen (1955), Barber *et al.* (1955) and Johnson (1953) have all been doing work of this type. Very few of the studies, however, have dealt with the relationship of juvenile to adult wood characteristics.

While working on environmental and genetic studies of the wood specific gravity of loblolly pine (*Pinus taeda* L.), Zobel and Rhodes (1955) noticed that mature trees which had wood with a high specific gravity tended to have a higher specific gravity in the wood of the first formed rings (i.e., juvenile wood) than mature trees having wood with a lower specific gravity. Similar observations had been reported by Australian workers such as Dadswell and Fielding on tracheid length of Monterey pine (personal communications). Based on preliminary sampling observations, it was felt there might also be a relationship between the specific gravity of the limbs of a seedling and the specific gravity of its bole wood (juvenile wood). Such a relationship between limb and bole of seedling has been reported for fiber length by Fielding.

The authors are, respectively, Silviculturist and Associate Forestry Educator, Texas Forest Service, College Station, Texas.

Objectives of the Research

The study was initiated to determine:

1. The degree of correlation between the specific gravity of the center, first-formed wood (juvenile wood) of a tree and its over-all wood specific gravity at maturity. Using mature trees, and working "backward", the specific gravity of the wood of a mature tree might thus be estimated from the specific gravity of its juvenile wood.
2. Whether a method can be devised to obtain juvenile specific gravity from the bole of a young tree or seedling by means of limb samples?

If these objectives yield positive results with high correlations, it will then be possible, by combining the findings, to predict the specific gravity of the wood of a mature tree from that produced by the tree when young, without destroying the young tree in the sampling process.

Experimental Procedure

Objective 1, the determination of the relationship between juvenile and mature wood of the same tree, was approached with two different groups of trees as the sampling populations. Sufficient data were collected for this phase of the experiment to obtain reliable results.

The first group of 92 loblolly pine trees were dominants and codominants on a rather uniform site. The stand was essentially even-aged, averaging 42 years at breast height (range 38 to 47). The trees comprise a five-acre seed production area, only the best trees having been left in the stand. All inferior, scrubby and crooked trees had been removed a few months prior to sampling.

The second group consisted of 106 trees from different sites. The trees were from 25 to 70 years of age (average 40 years), and were located throughout East Texas and the Lost Pines.[1] Table 1 gives the relative age distribution for the Group II trees. These trees were selected on the basis of their extremely high or extremely low wood specific gravities and are being used in genetic studies on the inheritance of wood specific gravity. The two groups represent the varied conditions shown in Table 2.

TABLE 1. Age distribution of Group II trees.

Age	Number of trees sampled
25–29	31
30–34	18
35–39	7
40–44	12
45–49	15
50–54	7
55–59	5
60–64	4
65–70	7
Total	106

Each tree was bored at breast height with the oversize (8 mm.) increment borer (Figure 1). From these increment cores, the specific gravity of the radius was determined. Then the specific gravity of the wood produced the first eight years was determined. From these two specific gravity measurements, it was possible to determine the degree of correlation between the

TABLE 2. Characteristics of trees studied.

	Group I	Group II
Age	even-aged (42 years)	25–70 years (ave. 40)
Site	uniform	diverse
Type of tree	dominant and codominant	dominant and codominant
Wood specific gravity	average for stand	selected extremes
Average specific gravity of full core	0.546	0.543
Average specific gravity of juvenile wood	0.527	0.518
Range of specific gravities of radial cores	0.640–.455	0.671–.429

[1]The Lost Pines is an area of isolated loblolly pines growing about 100 miles west of the southern pine region, under conditions of poor site, low rainfall and high temperature.

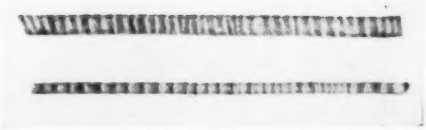

FIGURE 1. *Comparison of the oversize (8 mm.) increment core and the standard size increment core. The larger borer gives a greater wood volume for specific gravity determinations and also enables the obtaining of whole, uncut fibers.*

FIGURE 2. *Increment core showing the "juvenile" wood, right of the break as contrasted to the full radius core. Correlations were determined for the specific gravity of this juvenile portion in comparsion to the specific gravity of the full radius core.*

FIGURE 3. *Sample sections in the analysis of seedlings and small trees. The first branch section was obtained near the main stem of the tree, the last was from the last "old" wood near the end of the branch. Best correlations were always obtained using the limb sample nearest the main stem.*

specific gravity of the juvenile wood (first eight years in this experiment) and the specific gravity of the entire core.

The method here used introduces a certain amount of automaticity, in that one portion of the core is used for both calculations. The degree of automaticity will be dependent on the age and diameter of the tree (Table 1).

The term juvenile wood as used in this paper refers to the wood first formed around the pith. Many authors as Pillow (1954); Pillow, Terrell and Heller (1953); Scott and MacGregor (1952); Spurr and Hsuing (1954); Paul and Smith (1950); Bisset, Dadswell and Wardrop (1951), and a host of others recognize the special characters of such early formed wood. It usually has excessively wide rings, short fibers, high fibril angle, and a low specific gravity. Zobel and Rhodes (1955) found a considerable increase in the specific gravity of a radial core when the wod produced the first eight years was excluded from the specific gravity determinations.

The decision to define the first eight rings as juvenile wood was made solely on the basis of a visual study of a great many cores of normal second growth loblolly pine in East Texas. On the average, for second growth stands, a change to mature from juvenile wood takes place about the eighth year. For stands of other species or stands of loblolly in other regions, a value other than eight might be most suitable.

As illustrated by Figure 2, it was not always possible to hit the tree pith with the large borer. If it appeared that the pith was missed by one ring, the juvenile wood was then taken as the first seven countable rings. In a few cases two rings were missed. In the majority of cases, however, the pith was obtained. Juvenile wood, as defined, in no case included wood that was produced after the eighth year of growth.

The second objective, to determine if an estimate of juvenile wood can be obtained

from a young tree or seedling without destroying it, was attempted on a limited scale with three types of trees. Results must be viewed as exploratory in nature. Additional tests are underway. Thirty trees of each of three height classes (three feet, six feet, and nine feet) were selected. No suppressed or otherwise abnormal trees were used. The sample was obtained in the following manner:

a. Nine-foot trees.—A limb was selected from the tree as near breast height as possible. One sample was taken at the base of the limb and another from the last firm wood at the terminal. Both samples were six inches long. A six-inch section of the main stem was then removed. This sample included three inches of the stem above and three inches below the point of attachment of the sampled limb (Figure 3). Specific gravities of this stem and of two twig samples were determined and a correlation calculated between each twig sample and the stem's wood. (This stem wood will be juvenile wood in the mature tree.)

b. Six-foot trees.—These were handled and sampled as for the nine-foot trees.

c. Three-foot trees.—A limb was taken where available but only one six-inch sample obtained. Then the six-inch portion of the stem from which the limb arose was removed.

In order to obtain accurate specific gravities of the limb samples which were not uniform in shape, their volume was obtained by the water displacement method. In all other ways the method for calculation of specific gravities was as described by Spurr and Hsuing (1954).

Results of Study

The study was limited to loblolly pine in East Texas, and thus the results are directly applicable only to this area.

High correlations were found between the specific gravities of juvenile and mature wood for loblolly pine. The correlation coefficients were 0.805 for the 92 trees in the seed production area (Group I) and 0.856 for the 106 trees representing extremes in specific gravity (Group II). Both values were significant at the 1 percent level.

Although the inner core of juvenile wood has a lower specific gravity than that of the entire core (including the juvenile wood), it may be used to estimate the specific gravity of the mature tree with a reasonable degree of accuracy.

Although the specific gravity of the first eight rings is generally lower than that of the entire radius, it exceeded the specific gravity of the entire core for trees with the highest radial specific gravity. Figures 4 and 5 both illustrate this trend, which occurs above a juvenile specific gravity of about 0.60. The relationship between juvenile and total specific gravity thus tends to be curvilinear rather than linear.

No ready explanation is had for this trend. It is conceivable that some of the high juvenile specific gravities result from the presence of abnormal wood or deposits. All cores were checked for both compression wood (Forest Products Laboratory, 1953) and pitch, however, and those that had more than a very small amount of either were discarded.

The correlations between stem sections of seedlings and adjacent limb sections are given in Table 3. Highly significant correlations exist between the wood specific gravity of limbs and that of the bole where the limb arises. This correlation was not quite as high when the limb sample was taken near the end of the limb, but it is still statistically significant. Note the graph, Figure 6.

TABLE 3. Correlation coefficients (r) between stem and limb sections.

Seedling class	No. trees	Limb section Adjacent r	Terminal r
3-foot	30	.772	.....
6-foot	29	.692	.596
9-foot	30	.554	.537

All correlation coefficients significant at 1 percent level.

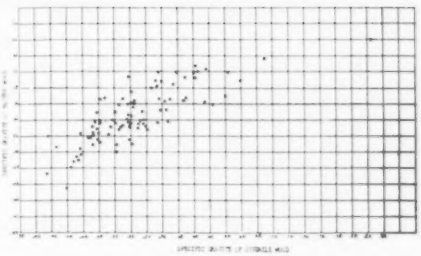

FIGURE 4. *Relation of wood specific gravity of mature (entire core) tree to that of the juvenile (first eight rings) growth for 92 trees in the uniform group (I). r = .805.*

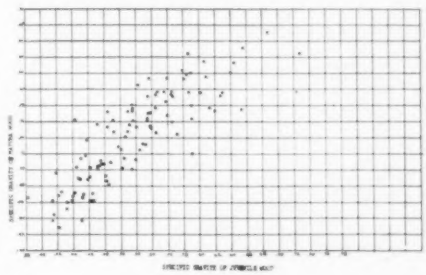

FIGURE 5. *Relation of wood specific gravity of mature (entire core) tree to that of the juvenile (first eight rings) growth for 106 trees in the diverse group (II). r = .856.*

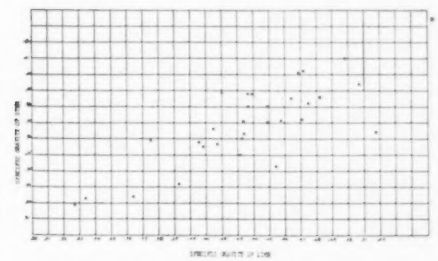

FIGURE 6. *Relation of wood specific gravity of the stem to that of the adjacent limb section for 30 three-foot trees. r = .772.*

These data indicate that it should be possible to estimate the specific gravity of a seedling or young tree from a limb of the tree, thus obtaining the specific gravity information without destroying the test tree or seedling.

Discussion and Summary

In order to speed up research in inheritance of specific characters, it is desirable to find young or juvenile characters which can be correlated with mature characters. The study reported here shows that for loblolly pine in East Texas, the specific gravity of the tree's wood can be so predicted. Highly significant correlations were found between the specific gravity of the wood of a young tree (the so-called juvenile wood found in the first eight rings in the mature tree) and the overall specific gravity of the wood of the mature tree. This relationship opens up many possibilities of estimation of specific gravity of the mature wood that will be produced by young trees, of obtaining an estimate of the specific gravity of the progeny of selected trees and hybrids, and of assessing the results of controlled crosses at an early age. Caution must be taken in the use of such estimates, since the relationship may be found to vary from area to area and site to site. For this reason, the research reported here does not constitute a blanket "formula" for southern pines or for loblolly pine. Further tests must be made to elaborate on these results obtained in East Texas. But the important fact is that a study of the young or juvenile wood has given a good estimate of the wood of the mature tree.

The second part of this study shows that an estimate of the specific gravity of the juvenile or young wood can be obtained from limbs of seedlings or young trees without destroying them. This relationship permits progeny tests, the results of crossing experiments and other young trees to be roughly assessed at an early age while still allowing the trees to grow. The final indisputable test remains, of course, the specific gravity of the wood of the tree

after it has matured. This short-cut in analyzing one wood property should be encouraging to the search for other short-cuts, thus reducing one of the main obstacles to forest genetics research, i.e., the time which must pass before data can be obtained and analyzed.

One inconsistency must be noted in this study. In the first test, the juvenile wood of mature trees was taken as the first eight years of growth near the pith. The bole wood of trees for which the limb correlations were determined in the second test, however, contained fewer than eight rings in almost every case. Juvenile wood, therefore, is defined somewhat differently in the two correlation trials. Additional studies underway will bridge this gap to determine if the difference in definition will be of importance.

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Foliage Symptoms as Indicators of Potassium-Deficient Soils

BY
LAURENCE C. WALKER

THE FORESTER who is going to plant trees on abandoned farm land needs to know what species are suitable to a given area. For this purpose, an analysis of the leaves of native vegetation, including (1) the determination of the chemical composition of the leaves, and (2) the observation of symptoms of nutrient deficiencies, has been found useful. A previous paper (Walker, 1955) reported chemical analyses relating the amount of potassium (K) in the foliage of various plants to the availability of potassium in the soil. The present paper discusses visible symptoms of nutrient deficiency attributed to a shortage of potassium. The ultimate aim of these studies is the development of a method for recognizing potassium deficiency in abandoned farm land so that the forester may avoid planting species that require susbtantial amounts of potassium.

Experimental Areas

Sand plains of glacial outwash origin occur extensively within the Adirondack Mountains of New York. Under the native vegetation, these coarse-textured acid soils develop weak to medium podzolic characteristics. Basic nutrients, particularly potassium, except for the portion retained by the organic component, are leached from the solum as rapidly as they are released by mineral decomposition.

Conifers were planted on abandoned farmlands on many of these plains in the 1930's. In a few years it was noted that the growth of white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Ait.), Norway spruce (*Picea abies* (L.) Karst.), and white spruce (*Picea glauca* (Moench) Voss) was severely retarded. These species developed small, chlorotic needles which did not last the usual time. Heiberg and White (1951) found these abnormalities indicative of K deficiency.

Exchangeable potassium in the plow horizon (upper 6 to 8 inches) in the plains ranges from 4.9 to 20.8 ppm. and averages 9 ppm. The potassium content diminishes to 2 ppm. in the upper *B* horizon and remains constant to the B_3 at about 4 feet. Only a trace of acid-soluble phosphorus occurs in the plow layer and upper *B* horizons. At lower depths, the phosphorus content is as much as 12 ppm. The pH increases with depth from 5.3 in the surface soil to 5.7 in the B_3. Nitrogen averages 0.13 percent in plow zones, while organic matter averages 4 percent. As expected, organic matter is closely related to nitrogen in these soils. It is also related to exchangeable potassium: the amount of

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Excerpted and revised from a Ph.D. thesis presented to the faculty of the State University of New York, College of Forestry, at Syracuse, June 1953. The author is indebted to Professors D. P. White and S. O. Heiberg for helpful counsel. Prof. Walker is on the research staff of the School of Forestry, University of Georgia, at Athens.

mineral colloidal matter in coarse sands is too meager to have much effect on the supply of potash in ionic form. Hence, most of the available element is held on organic colloids.

Textural analysis of the plow zone showed that this material consisted of 89 percent sand, 6.4 percent silt, 0.8 percent coarse clay, and 3.8 percent fine clay (Heiberg and White, 1951). These sands belong to the Hinckley series. Other non-deficient brown podzolic soils belonging to the Gloucester, Cornwall, Hinckley and Essex series were studied for comparison.

Previous Investigations

Eckstein, Bruno, and Turrentine (1937), Wallace (1951), Bear *et al.* (1949), and McMurtrey (1948) have presented reviews of what was known about the foliar symptoms of nutrient deficiencies, chiefly in field and orchard crops. A monograph by Becker-Dillingen (1939) outlines some deficiency symptoms of forest trees in Europe.

Recently Heiberg and White (1951) found that potassium deficiency in red pine, white pine, Norway spruce, and white spruce produced short chlorotic needles which turned brown and died prematurely. Stone (1953) found that deficiencies of magnesium in sandy soils in which young red pine, white pine, and jack pine were planted resulted in a bright yellow discoloration of the tips of the needles in the fall.[1] Lafond observed similar magnesium deficiency symptoms for red pine in Quebec. It was suggested that this symptom is often accompanied by low levels of potassium.[2]

In some instances it was not until the third year after Stone applied magnesium fertilizer that the apical yellowing disappeared. A few trees then exhibited potassium deficiency symptoms. Conversely, magnesium deficiency symptoms were intensified by fertilizing with potassium. Kidson, Askew, and Chittenden (1940) observed a high percentage of potassium in leaves of trees severely affected by magnesium shortage. This suggests the importance of the K/Mg ratio in determining the severity of the magnesium deficiency. Deficiencies of potassium may also be accentuated by the presence of large amounts of nitrogen in available form in the soil (Worswick, 1950), as stimulated growth results in increased requirements for potassium.

Chlorotic needles of white pine seedlings grown under low potassium conditions in sand media have been observed (Mitchell, 1939; Hobbs, 1944).

Some information is available regarding nutrient deficiency symptoms in herbs (Goodall and Gregory, 1947; Kitchen, 1948; Bear *et al.*, 1949). Generally, browning and curling of leaf margins, chlorosis, and premature leaf-fall are evident.

Certain precautions must be taken when deficiency symptoms alone are used for the diagnosis. Thomas (1945) warns that a color abnormality usually attributed to a particular deficiency may vary with temperature, light and moisture. Earlier, Möller had also stressed that seasonal variations in the mineral absorption of plants affect the time the symptoms appear. Drought, continuous strong winds, low temperature, and frost are known to produce marginal leaf scorch similar to that caused by a lack of potassium. Deficiencies of copper and manganese are also said to be difficult to distinguish from potassium deficiency (Worswick, 1950).

Wallace (1951) has presented the following general foliar symptoms of potassium deficiency:

1. dull bluish-green color
2. chlorotic, especially in intervenal areas
3. browning of tips and marginal scorching
4. brown spots first occurring on older leaves

Worswick also noted necrosis along

[1]Both Heiberg and White's and Stone's work was carried out in the vicinity of the present research.

[2]Personal communication from E. L. Stone, Cornell University.

TABLE 1. Potassium in foliage (dry-weight basis) and soil plow-layers.

Species	Deficient specimens			Normal specimens			Fertilized specimens	
	July percent	August percent	Soil ppm	July percent	August percent	Soil ppm	August percent	Soil ppm
Pinus strobus	0.44	0.27	10.1	0.67	0.46	26.4	0.57	33.7
Prunus serotina	.65	.55	9.8	1.07	1.26	26.4	1.64	33.7
Betula populifolia	.77	.71	10.1	.90	1.16	9.8	1.25	35.2
Acer rubrum	.59	.45	10.0	.66	.68	36.5	.96	46.5
Rubus subgenus Eubatus	.73	.65	12.4	1.21	1.11	38.7	1.57	48.9
Spartium scoparium	.....	.30	8.9	.....	.....	.....	1.31	49.9

midribs and veins and the presence of creamy-yellow coloration shading into yellow-green prior to scorching as symptoms of potassium deficiency.

Field Procedures

Four replicated sampling plots were established in each of 19 locales. In addition, plots fertilized with 200 pounds per acre of 60 percent potassium chloride were also installed.

Sampling varied for the several vegetative forms. Tree leaves were taken from east-facing branches at the crown middle of nine species. Leaves, including petioles, and needles were removed from branches in the field. Collections were made in early July and mid-August. Leaves of *Rubus* subgenus *Eubatus* spp. and *Fragaria virginiana* Duchesne were randomly collected. In addition to native vegetation, cultivated *Lupinus perennis* L., *Trifolium pratense* L., and *Spartium scoparium* W. were studied. Leaves of *Lupinus* and leaves and stems of *Trifolium* and *Spartium* were sampled in August. Soil samples were taken from the plow and *B* horizons.

Laboratory Procedures

Tissue samples were dried at 70° C. in an electric oven for 3 hours shortly after collection, then ground in a Wiley mill and dried at 70° C. in a circulating-air oven for 24 hours (White, 1954). Samples of dry tissue weighing 1.000 gm. were ashed at 500° C. for 3 hours, the ash dissolved with 2*N* nitric acid, diluted to volume, and the aqueous solution analyzed for potassium content with a Beckman flame spectrophotometer.

Soil samples were air-dried and passed through a 2mm. mesh sieve. Analyses were made in duplicate on air-dried soils. For exchangeable potassium determinations, a 50-gm. sample was leached with *N* NH_4Ac as outlined by Peech *et al.* (1947). The leachate was evaporated to dryness, treated with sufficient H_2O_2 to oxidize organic matter, acidified with 2*N* HNO_3, and subjected to flame spectrophotometric analysis. Total nitrogen was determined by a modified Kjeldahl method (Jackson, 1949). Analysis for acid-soluble phosphorus was by the $SnCl_2$-reduction method on an extract leached with 0.002*N* H_2SO_4. Oxidizable organic matter was measured by wet combustion using $H_2Cr_2O_7$ and H_2SO_4 with heat applied (Jackson, 1949). Hydrogen-ion concentrations were determined with a Beckman glass electrode pH meter using a soil-water "paste" (Peech *et al.*, 1947).

Results and Discussion

Symptoms of potassium deficiency varied with the species studied.[3] Table 1 shows the amounts of potassium found in deficient

[3]Kodachrome slides illustrating these symptoms may be borrowed or copies procured at cost from the author.

and normal specimens.

Prunus serotina. Striking and unusual discolorations in the foliage of black cherry were observed in the middle of August. Bright red margins extending almost to tip of the leaf and about one-half the distance to the midrib were produced. The line of demarcation between the pigmentation and normal coloration is well defined (Fig. 1). Trees so affected were limited to unfertilized plots, while those growing under fertilized conditions appeared normal. Almost all leaves on the trees were similarly discolored. By late September, the anthocyanin margins had widened and extended to the leaf tip; red color intensity also increased, and blue and violet hues were produced. The effect of autumnal coloration is quite distinct from this malformation.

None of the species of *Prunus* studied exhibited curling of the edges of leaves, an established symptom of potassium deficiency for orchard-grown varieties of *Prunus cerasus* L. (Wallace, 1951). Boynton and Compton (1945) found the critical value of potassium for *P. cerasus* in midsummer shoot leaves to be between 0.75 and 1.00 percent. Below this point, deficiency symptoms occurred.

FIGURE 1. *Abnormal coloration (red) at margins of potassium-deficient* Prunus serotina *leaf (right) and normal leaf (left).*

The abnormalities observed seem to result from potassium deficiency, but it is quite possible they are tied in with magnesium deficiency. While Wallace describes magnesium-deficient *Prunus cerasus* as containing pigmentation similar to that reported here, he states that in some cases it is difficult to distinguish between marginal necrosis resulting from magnesium deficiency and a similar condition resulting from a low supply of potassium. Boynton stated that in his experience this abnormal coloration more closely resembles potassium deficiency than magnesium but then followed his comment on the likelihood of either appearing on such soils.[4] Since magnesium deficiency may be induced by applying potassic fertilizers (Boynton and Compton, 1945; Lilleland and Brown, 1938), the fact that fertilization did not accentuate deficiency symptoms also substantiates the hypothesis. Similarly, according to Blank (1947), potassium deficiency accelerates anthocyanin formation.

Pinus strobus. Chemical analyses of needle tissue collected in July show that trees with deficiency symptoms as described by previous workers contained from 0.32 to 0.59 percent potassium and non-deficient trees from 0.53 to 0.84 percent. This decreased in August to between 0.19 and 0.38 percent for deficient and 0.40 and 0.55 percent for normal trees exclusive of fertilized individuals which had between 0.41 and 0.76 percent potassium in August foliage. Heiberg and White (1951) found from 0.45 to 0.74 percent potassium in mid-September collected needle tissue from healthy trees. At that time, they found a maximum of 0.34 percent potassium in current year's needle tissue for pines displaying deficiency symptoms. In

[4]Personal communication, *ibid.*

the present study, it was difficult to detect appreciable improvement in the foliage of fertilized trees noted to be potassium-deficient prior to fertilization in May. Elongation of new branches and needles as the season progresses tends to mask foliar symptoms of deficiency, particularly late in the season. Early spring seems to be the most appropriate time for ocular determination of low potassium levels for white pine. For this species, the diminution of potassium in needle tissue as the season progresses is quite clear-cut (Walker, 1955).

Betula populifolia. Chlorosis of the leaves of gray birch, beginning at the margins and proceeding inward, was noted in mid-August (Fig. 2).

The transition from yellowish-white chlorotic coloration to normal-appearing green tissue in leaves exhibiting deficiency symptoms is sharp in contrast to the gradual transition of colors in autumn foliage. In either case the yellowing probably results from the breakdown of chlorophyll and limitation of its production to expose yellow carotinoids.

From this limited study the critical potassium level for gray birch foliage may be tentatively set at about 1.00 percent. No deficiency-exhibiting leaves were found with more than 0.83 percent potassium and normal appearing foliage did not contain less than 1.00 percent when symptoms appeared.

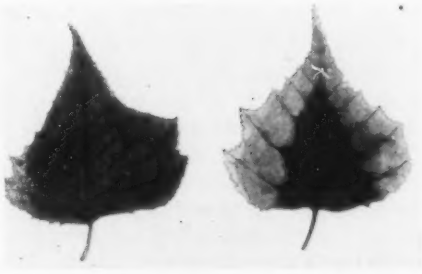

FIGURE 2. *Chlorotic margins of* Betula populifolia *leaf (right) with normal leaf (left).*

With the data at hand and the knowledge that magnesium deficiency is prevalent in soils of these areas, it is difficult to conclude that this symptom is solely that of potassium deficiency. The evidence does point in that direction, however, particularly since it has been shown that fertilization with potassium in sites low in available magnesium accentuates magnesium-deficiency symptoms. This did not occur in the present study.

Acer rubrum. Leaves on red maple trees in low-potassium soils were chlorotic throughout the summer. In fertilized plots, the foliage was notably greener than elsewhere. Chlorosis occurs throughout the leaf, but is slightly more pronounced at the margins. About 0.60 percent may be considered as the point below which potassium is in short supply and deficiency symptoms may be expected to appear. The range in August for leaf potassium in deficient-appearing trees was from 0.29 percent to 0.66 percent and in healthy-appearing trees from 0.56 percent to 1.11 percent. Bard (1945) found potassium ranging from 1.02 percent to 1.16 percent potassium in leaves sampled in late summer from trees grown in soils fertilized with over 200 pounds per acre (100 ppm) exchangeable potassium.

Rubus subgenus Eubatus spp. Coloration was observed on leaves of these plants similar to that noted by Wallace (1951) for *Rubus occidentalis* L. Marginal browning extended between veins, practically to the midrib, and growth appeared poor. This midsummer abnormality resembles very closely the natural coloration of foliage in autumn. In fact the resemblance makes visual distinction late in the season virtually impossible. It is quite probable that under both conditions the leaves are in similar

states physiologically, anthocyanin pigmentation having been exposed as a result of destruction of chlorophyll molecules. It is suggested that, for this species, the critical potassium level below which deficiencies may be expected is 0.80 percent.

Wood (1947), working with cultivated *Rubus occidentalis*, discovered potassium deficiency symptoms in older leaves. They turned brown at edges and tips, then curled, and finally turned black. He, as well as the present writer, found no relationship between the amount of exchangeable potassium in the soil and the concentration of the element in leaves of this species.

Spartium scoparium. This European legume exhibited symptoms of potassium deficiency which were substantiated by fertilization and quantitative analyses of that element in the plant. General yellowing and chlorosis of leaves beginning at the base of the plant and the bases of leaves and leaflets, stunting of plants, and reduction in size of leaves were characteristics of plants seeded a year prior to sampling in an abandoned field (Fig. 3). Fertilizing with 200 pounds per acre of KCl in May following the year of planting had, by mid-August, resulted in normal-appearing plants. The foliar potassium level increased four-fold.

Miscellaneous. Analyses of *Pinus banksiana* foliage support Stone's (1953) conclusion that needle-tip chlorosis of this species in the Adirondack area is due to low magnesium levels rather than to potassium deficiency. The amount of potassium in deficient-appearing and healthy needles sampled did not differ significantly. The average was 0.38 percent.

Fertilized and unfertilized *Fragaria virginiana*, *Lupinus perennis*, and *Trifolium pratense* exhibited leaves similar to those which, when produced by cultivated plants, are described in the literature as being potassium deficient (Eckstein, Bruno, and Turrentine, 1937; Kitchen, 1948; and Morgan, 1948). But there is no evidence that these abnormal coloration symptoms are reliable as indicators of potassium deficiency in reforestation sites.

FIGURE 3. *Chlorosis of* Spartium scoparium *leaf (right) and leaf from K-fertilized plant (left).*

Conclusions

From this exploratory study, practical application is evident. The use of demanding species (white pine, red pine, white spruce, red spruce) for plantation establishment on sites where potassium-deficiency symptoms are observed or where exchangeable potassium in soil plow layers is less than 20 ppm would be poor silviculture unless fertilization was anticipated. A somewhat lower value may be inferred from the data presented by Heiberg and White (1951).

Sites presently occupied by species with deficiency malformations have responded favorably to 200 pounds per acre of 60 percent KCl. Subsequent treatments may be necessary, but the economics of that procedure is beyond the scope of this paper. Yet, Galoux (1954) considers it both practical and economical to fertilize impoverished soils with potassium prior to establishment of scotch pine and spruce plantations in France. In the low potash areas of the present study, however, less demanding conifers such as Scotch and jack pines are recommended for infertile fields to aid the restoration of site potential for later succession by more demanding and more valuable species.

Summary

Abnormal colorations indicative of potassium-deficient soils were observed in foliage

of *Prunus serotina*, *Betula populifolia*, *Acer rubrum*, *Pinus strobus*, and *Rubus* subgenus *Eubatus* spp. For the first species, a strikingly bright-red pigmentation occurred at leaf margins. *Betula populifolia*, when potassium-deficient, exhibited leaves with chlorotic margins sharply delineated from normal-appearing green tissues. *Acer rubrum* foliage was uniformly chlorotic. Needles of *Pinus strobus* were short, chlorotic, and often brown at tips. Leaflets of *Rubus* subgenus *Eubatus* spp. displayed marginal browning which extended between veins practically to the midrib. Foliage of cultivated plants (*Lupinus perennis*, *Trifolium pratense*, and *Spartium scoparium*) exhibited abnormal coloration, but except for *S. scoparium* the leaves of which were chlorotic, this could not be attributed to potassium nutrition alone. On sites where these deficiency symptoms are exhibited, stunted growth of the more demanding conifers is also likely to occur. Critical values for potassium concentration in mid-August collected leaf tissue below which deficiency symptoms may be expected are as follows:

Prunus serotina	0.8 percent
Betula populifolia	1.0 percent
Acer rubrum	0.6 percent
Pinus strobus	0.4 percent
Rubus subgenus *Eubatus* spp.	0.8 percent
Spartium scoparium	0.3 percent

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Colchicine

Colchicine—in agriculture, medicine, biology, and chemistry. By O. J. Eigsti and Pierre Dustin, Jr. 1955. 470 pp. Iowa State College Press, Ames, Iowa.

Review by Roland E. Schoenike
Southern Forest Experiment Station, U. S. Forest Service.

Many workers in plant genetics have wished for a comprehensive synopsis of what is known about colchicine. This is such a book.

The authors are well qualified. Albert Pierre Dustin, father of the junior author, initiated the modern era in colchicine research by showing that the drug arrests mitotic division in animal cells. This was followed by hundreds of experiments to demonstrate that the phenomenon occurs in almost all biological material. Pierre Dustin, Jr., continued the work after his father's death. In 1937 the senior author discovered the most striking and important effect of colchicine, the induction of polyploid cells, by treating onion root tips with the drug. The next five years saw a tremendous increase in polyploid research. For a while, such research became what the authors describe as a colchicine fad.

The book can be understood, in the most part, by persons with only a smattering of genetics. Terminology is handled well, particularly in dealing with the polyploid problem. Subjects are arranged logically and treated clearly. Chief objections are an unevenness in style, a tendency toward repetition, especially in the earlier chapters, and possibly the overstressing of some experimental work such as the 1934 experiments of A. P. Dustin. Documentation is exceptionally thorough; each chapter contains 50 to 300 references, including many personal communications. The illustrations are carefully chosen and printed on high-quality paper.

The book reviews all aspects of the subject. Three chapters are devoted to the pharmacology and pharmacognosy of the drug, three to its effects on plant and animal cells, and one to its chemistry. Several chapters deal with its effects on animals and humans. Five valuable chapters are concerned with polyploidy. A short chapter on techniques for handling the drug is followed by a longer one discussing the specific effect of colchicine on cells.

The book is essential for persons engaged in colchicine research, and perhaps also for geneticists and cytologists generally. It should be of interest to plant and animal physiologists, pathologists, and histologists. Biochemists can profit from several chapters. In short, it touches on many major areas of research.

Growth of Forest Plantations on Different Soils of Finland

BY
ALBERT L. LEAF

THIS PAPER is concerned with the relationship between the growth of plantations, composition of soil, nutrient content of foliage, and floristic types of different parts of Finland. The investigated plantations were located on six floristic types, established in accordance with the classification of Cajander (1909, 1949); *Empetrum-Vaccinium*[1] and *Hylocomium-Myrtillus* in North Finland, and *Vaccinium, Myrtillus, Pyrola,* and *Oxalis-Mytillus* in South Finland. According to Aaltonen (1941), the *Pyrola* and *Oxalis-Myrtillus* types have a higher productive potential than other types studied, confined to coarse-textured soils.

The northern part of Finland is a cool and humid region with predominance of podzolized soils. The climate of the southern portion of the country is milder and podzolization is less pronounced. Many investigated soils are influenced by a ground water table. In some localities the process of podzolization is masked by infiltration of dark colored humates with subsequent development of profiles resembling mull soils.

Methods of Analyses

The study included nine Norway spruce (*Picea abies*, L.) and twenty Scotch pine (*Pinus sylvestris*, L.) plantations varying in age from 20 to 50 years. These were distributed as follows: seven plantations in North Finland on the Arctic Circle; seven plantations in Central Finland near Lyly; eight plantations near Elimäki in Southeastern Finland, and seven plantations near Salo in Southwestern Finland. The method of appraisal adapted in Wisconsin studies (Leaf and Keller, 1956) was modified in accordance with suggestions of Finnish specialists. Information on history of plantations, such as time and method of establishment, rate of growth at different periods, and silvicultural treatments, was provided by the Forest Research Institute in Finland. The plantations of Scotch pine were largely established by spot or broadcast seeding, usually after burning; the plantations of Norway spruce originated by the use of 2-2 nursery stock.

The genetic nature of soils, their structural characteristics, and the position of the ground water table or gley horizon were

[1] "Vaccinium" refers to *Vaccinium vitis-idaea*, whereas "Myrtillus" refers to *Vaccinium myrtillus*.

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determined by excavations of soil trenches. Since the content of available nutrients in soils of plantations is concentrated in the surface soil, sampling of soil was not extended beyond the upper six inch layer enriched in humus. The samples were collected by means of a calibrated tube. The content of skeletal material was determined in the field (Viro, 1947, 1952).

Samples of foliar tissues for the determination of their nutrient contents were collected in the fall from the last year's terminal leader. Three sample trees of average heights and diameters from each plantation were subjected to stem analyses. In plantations with pronounced differentiation of height growth, the measurements were confined to dominant and codominant trees. The average rate of growth was determined from graphically interpolated results of stem analyses.

The following determinations were made in the laboratory: soil texture, content of organic matter, pH value, and contents of the total nitrogen, available phosphorus, available potassium, and replaceable calcium and magnesium. The analytical procedures of the Forest Research Institute in Finland[2] and Wisconsin State Soils Laboratory (Wilde and Voigt, 1955) were used. The concentration of different elements or oxides was determined either colorimetrically or spectrophotometrically. The foliage was analyzed for the pH value, and contents of ash, nitrogen, phosphorus, potassium, calcium, and magnesium.

Results of Mensuration Analyses

Figure 1 presents average rates of height growth of pine and spruce plantations on different forest types established according to the Finnish classification. The growth rates of pine on *Myrtillus* and *Vaccinium* types, recorded in this survey, coincide closely with the results obtained by Lönnroth (1925) and Ilvessalo (1926). For comparison of the rate of growth of trees on different types, the average heights and diameters at the age of 20 years were determined from the results of the stem analyses (Table 1). Because many plantations studied were previously subjected to thinnings, the diameter growth does not express the productive potential of the site. On the other hand, the height growth of both spruce and pine plantations is strikingly correlated with different forest types.

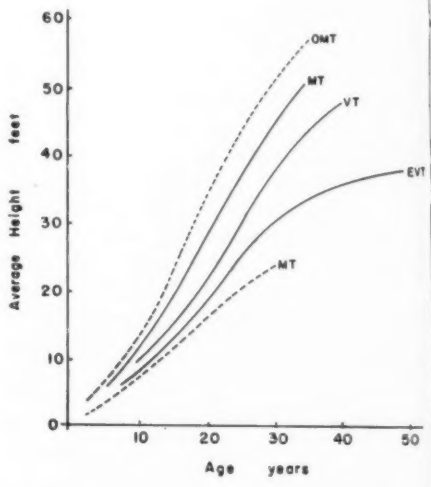

FIGURE 1. *Average rate of height growth for Scotch pine and Norway spruce plantations on different forest types in Finland: OMT*—Oxalis-Myrtillus, *MT*—Myrtillus, *VT*—Vaccinium, *and EVT*—Empetrum-Vaccinium. *The solid line denotes pine plantations and the broken line denotes spruce plantations.*

[2]Unpublished procedures for the determination of available nutrients in forest soils and total nutrients in plant tissue, Department of Forest Soils, Forest Research Institute in Finland, Helsinki, Finland (1955).

TABLE 1. Average growth of Scotch pine and Norway spruce plantations at 20 years of age on different forest types in Finland, as interpolated from stem analyses. Standard errors are given with the exception of cases where sampling was insufficient for statistical analysis.

Forest Types	DBH	DBH Growth per year	Height	Height Growth per Year
	inches		feet	inches
		Scotch pine plantations		
Empetrum-Vaccinium	2.4	0.12	18.0	10.8
Hylocomium-Myrtillus	2.8 ± 0.2	0.14 ± 0.02	19.1 ± 1.3	12.0 ± 0.9
Vaccinium	2.2 ± 0.1	0.11 ± 0.01	21.7 ± 1.9	12.8 ± 0.3
Pyrola	2.8 ± 0.1	0.14 ± 0.04	25.4 ± 1.1	15.2 ± 0.6
Myrtillus	5.4	0.27	26.8	16.1
		Norway spruce plantations		
Myrtillus	3.0 ± 0.2	0.15 ± 0.01	15.6 ± 1.2	9.4 ± 0.8
Pyrola	2.8	0.14	21.0	12.6
Oxalis-Myrtillus	3.5 ± 0.1	0.18 ± 0.01	30.8 ± 1.3	18.5 ± 0.8

Results of Soil Analyses

The characteristic morphology of soil and the approximate position of the ground water table observed in different investigated floristic sites is presented graphically in Figure 2. In broad terms, *Empetrum-Vaccinium*, *Hylocomium-Myrtillus*, and *Vaccinium* floristic sites are confined to podzolized deposits of moraines or partly assorted fluvial-glacial pitted outwash. *Hylocomium-Myrtillus*, *Myrtillus*, and *Oxalis-Myrtillus* types occur on mid-gley soils characterized by the presence of gley layer at a depth varying from 18 to 27 inches. *Pyrola* type is characterized by ground water table approach the A_2 horizon of soil and may be rated among hydromorphic or even semi-swamp soils (Wilde, 1940). The observed genetical characteristics are strictly confined to the investigated plantations and no generalization is intended to cover the broader range of Finnish soils.

The results of particle size analyses (Table 2) present a clear picture of the distribution of forest types in relation to the textural composition of soils. Thus *Empetrum-Vaccinium* and *Hylocomium-Myrtillus* types are confined to coarse textured soils, whereas *Pyrola* and *Oxalis-Mytillus* types to fine textured or loam soils; the *Vaccinium* types of both *vitis-idaea* and *myrtillus* species occupy intermediate, sandy loam soils. The textural properties and the corresponding water holding capacity of soils appear to exert an influence on the supply of soil organic matter. *Oxalis-Myrtillus* and *Pyrola* types appear to be the least inducive to rapid breakdown of organic remains and consequently these soils exhibit the highest content of organic matter. The *Vaccinium* types retain in the surface layer an amount of humus that should be considered satisfactory for all trees of the podzolic region. The *Empetrum-Vaccinium* and *Hylocomium-Myrtillus* types show the lowest content of humus. The reaction of the soil, varying for all types within the narrow limits of pH 4.8 to pH 5.4, is not a factor of ecological significance in the plantations studied. As may be expected, the supply of essential nutrients parallels that of the textural composition and organic matter content of the soils. However, some slight deviations occur in the levels of P_2O_5 and K_2O con-

TABLE 2. Average analytical data of the surface (0-6 inches depth) soil of Scotch pine and Norway spruce plantations on different forest types in Finland. Calculation of standard errors is omitted in cases where sampling was insufficient.

Forest Tynes	Soil Fractions: Larger than 2.0 mm. Percent	Soil Fractions: Smaller than 0.05 mm. Percent	Organic Matter Percent	Reaction pH (Medians)	Total N Percent	Available Nutrients: P_2O_5 ppm.	Available Nutrients: K_2O ppm.	Available Nutrients: CaO me./100 g.	Available Nutrients: MgO me./100 g.
Scotch pine plantations									
Empetrum-Vaccinum	36.6	11.3	2.6	5.1	0.065	8	62	0.39	0.13
Hylocomium-Myrtillus	32.8±6.1	9.7±2.0	2.4±0.2	4.9	0.061±0.006	17±2	60±4	0.51±0.07	0.19±0.02
Vaccinium	20.3±3.7	15.4±2.9	4.3±0.8	4.8	0.111±0.023	18±3	108±26	0.60±0.09	0.26±0.05
Pyrola	None	45.8±2.5	9.4±1.3	5.3	0.247±0.033	19±1	148±31	1.38±0.23	0.90±0.13
Myrtillus	17.4	17.5	4.5	4.9	0.112	17	79	0.81	0.37
Norway spruce plantations									
Myrtillus	26.5±3.7	18.2±0.3	4.8±0.8	4.9	0.120±0.020	19±2	77±27	0.78±0.36	0.30±0.14
Pyrola	None	44.8	8.3	5.4	0.209	18	114	1.08	0.64
Oxalis-Myrtillus	2.6±1.4	66.2±6.3	23.6±7.3	5.1	0.607±0.165	27±6	156±25	1.58±0.25	1.08±0.17

tents. The content of MgO is directly proportional to that of CaO. Within the limits of plantations studied, soils of Finnish forest types showed a very close correlation between the rate of growth and composition of soils, as well as the ground cover vegetation.

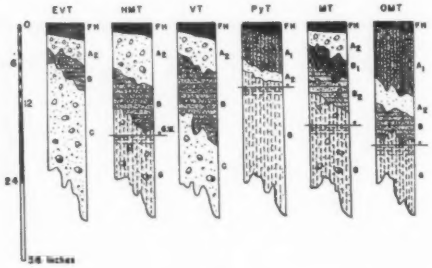

FIGURE 2. *Profiles of genetical soil types of different investigated floristic types in Finland: EVT*—Empetrum-Vaccinium, *HMT*—Hylocomium-Myrtillus, *VT* — Vaccinium, *PyT*—Pyrola, *MT*—Myrtillus, *and OMT*—Oxalis-Myrtillus.

As pointed out by Aaltonen (1948), the relationship between the rate of tree growth and content of soil nutrients are often complicated by the supply of soil moisture or conditions of drainage. This is particularly true of *Vaccinium* and *Myrtillus* types. In many instances, the tree growth on *Myrtillus* type, well supplied with water, is higher in spite of the lower content of nutrients than is found in soils of *Vaccinium* type occurring on uplands often deficient in moisture. The growth of Scotch pine in the lowlands of South Finland increases from *Pyrola* to *Myrtillus* types while the growth of Norway spruce exhibits a reverse tendency. This trend is in accord with the differences in the colloidal content and position of the ground water level in soils of these types, as well as with the inherent abilities of spruce and pine to tolerate stagnation.

Results of Foliar Analyses

Results of analyses of terminal leader needles, collected from plantations of comparable age are given in Table 3. These results suggest a fairly close correlation between nitrogen contents of the foliage and the rate of tree growth, as previously observed by Aaltonen (1948; 1950). The low content of nitrogen in the foliage may

TABLE 3. Analytical data of the terminal leader foliage of Scotch pine and Norway spruce plantations varying from 34 to 38 years of age on different forest types in Finland.

Forest types	Reaction pH (Medians)	Ash	N	P_2O_5	K_2O	CaO	MgO
		Percent					
			Scotch pine plantations				
Hylocomium-Myrtillus	5.2	2.41	1.439	0.49	0.89	0.49	0.25
	4.7	2.42	1.173	0.49	0.66	0.48	0.19
Vaccinium	4.6	2.22	1.445	0.47	0.57	0.42	0.21
	4.9	3.19	1.462	0.41	0.82	0.74	0.25
Pyrola	5.2	2.62	1.949	0.47	0.58	0.41	0.28
Myrtillus	5.1	2.95	2.105	0.86	0.82	0.34	0.24
			Norway spruce plantations				
Myrtillus	3.7	3.53	1.142	0.36	0.81	0.61	0.30
Oxalis-Myrtillus	4.3	4.79	1.428	0.59	0.82	1.07	0.37
	4.2	5.52	1.333	0.42	0.96	0.78	0.34
	4.1	3.57	1.218	0.35	0.81	0.64	0.33
	4.4	4.27	1.372	0.43	1.19	0.57	0.40
	4.1	3.03	1.218	0.40	0.96	0.43	0.30

occasionally result from the burning of the humus layer.

The results of foliar analyses of other nutrients failed to show any relation to floristic type, rate of tree growth, or nutrient supply of soils investigated. The average length of the terminal leader foliage of pine progressively increased from a minimum of 1.76 inches on *Empetrum-Vaccinium* type to a maximum of 3.00 inches on *Mrytillus* type. No definite trend in the length of spruce needles was detected. The Norway spruce foliage had a more acid reaction, higher ash content, and generally higher content of nutrients, especially CaO and MgO, than the Scotch pine foliage.

Conclusion

The study included nine Norway spruce and twenty Scotch pine plantations varying in age from 20 to 50 years located on six floristic types: *Empetrum-Vaccinium* and *Hylocomium-Myrtillus* in North Finland, and *Vaccinium*, *Myrtillus*, *Pyrola*, and *Oxalis-Myrtillus* in South Finland. A close correlation was detected between the forest types, as defined by the Forest Research Institute in Finland, and the rate of growth of plantations. Analyses of soils revealed also a close relationship between the site quality of plantations and several important soil characteristics, such as texture, content of organic matter, and supply of available nutrients. The reaction preserved its value of about pH 5.0 in soils of all types studied. Foliar analyses, performed on the terminal leader foliage, indicated a fairly close correlation between nitrogen contents of the foliage and the rate of tree growth. No relationship between content of nutrients in foliage and the supply of available nutrients in investigated soils was detected. The average length of the terminal leader needles of Scotch pine reflected conspicuously the level of soil fertility, increasing from 1.76 inches on *Empetrum-Vaccinium* type to 3.00 inches on *Myrtillus* type.

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Forestry Dictionary

We are informed by the Swedish Forestry Association that a second revised edition of the Swedish-English-German-French Forestry Dictionary by M. E. Simonen (recently reviewed in FOREST SCIENCE, vol. 1, no. 2/-1955) has recently been published. As before, the Dictionary can be ordered from Svenska Skogsvardsföreningen, Regeringsgatan 18, Stockholm C, Sweden. Price $6.80.

Forest Policy in Scandinavia

Public Policy Toward Private Forest Land in Sweden, Norway, and Finland. By R. E. Marsh. The Charles Lathrop Pack Foundation, Washington, D. C. 1954. 80 pp., illustrations. $1.00.

Review by Prof. Thorsten Streyffert
Dean, Royal College of Forestry, Sweden

The author of this report spent about 3 months in Sweden, Norway, and Finland in 1951, studying public policy toward private forest land on behalf of the then Chief of U. S. Forest Service, Lyle F. Watts. His report is undoubtedly the most thorough and well-balanced analysis so far made by a foreign student of this somewhat complicated problem.

The publication should therefore provide an excellent opportunity to the American reader who is interested in finding ways and means to solve the problem of American public policy toward private forest land and to become acquainted with the principles and methods that have proved fairly successful in the Nordic countries.

Credit is due to the author for the care he has taken to make sure that these principles and methods can be applied in the United States. He points out the differences between the United States and the Nordic countries in their economic, social, and political environments. The prominent place of forestry in the national economy of these countries is stressed. Therefore, the whole population including the forest owners consider forestry from a national viewpoint. This attitude is reinforced by more far-reaching government regulations than those in effect in the United States. The smaller size of the Nordic countries makes it easier to apply and administer a national forest policy than would be possible in a country like the United States with its large size, heterogeneous population, and diverse natural and economic conditions. For example, Sweden compares with California in size and population, and either Norway or Finland is smaller than Sweden.

These conditions hold true for the forests, which are much more uniform in the Nordic countries than in the United States. By way of comparison, there are only two species of major economic importance in the Nordic countries—the Scotch pine and the Norway spruce—supplemented by some hardwoods, of which birch is the most common.

For these several reasons the conclusion is reached that great caution must be exercised in applying the experience of Scandinavia and Finland to the United States. However, Marsh suggests that some of the principles and methods used in Scandinavia and Finland might be worth a trial in the United States.

The greater part of the time spent on this study was in Sweden, and the status of forest policy in Norway and Finland is compared with that in Sweden. Thus a comprehensive view of forest policy in the three Nordic countries is provided. Marsh considers forestry in Sweden to be somewhat more advanced than in Norway and Finland, partly because Sweden inaugurated her modern forest policy as early as 1905, before the other two countries. Although considerable differences in detail and in administrative apparatus exist, Sweden's forest policy seems to have been the general pattern followed by policies of Norway and Finland.

Basic Principles of Forest Policy in Scandinavia and Finland

Forest policy in all the Nordic countries is based on the same three basic principles. (This is true in many other countries, as well.) These principles are legislation, grants-in-aid, and education and advice. The fact that this policy was applied somewhat earlier in Scandinavia and Finland than in most other countries may partly explain the fairly good results so far achieved. The main reason for these results, however, must be sought in the environment itself and in the way the forest policy has been adapted to make the most of its environment.

Coordination of the three basic principles in carrying out forest policy is greatly stressed by the author. First and foremost, education and advice are used to guide and help forest owners. Next in importance are grants-in-

aid, restricted mainly to forestry work not required by law, such as draining marshlands and swamps, and artificial regeneration on old, bare lands. Only when these methods fail, and in comparatively few cases, is there resort to the compulsory provisions of law.

Cooperation with Forest Owners

Governing bodies in the three Nordic countries cooperate with forest owners in different ways. In Sweden the central administration of forest policy is vested in the Private Forestry Board in Stockholm. The field work, however, is carried on by local boards, one in every county (25 in all). Cooperation with forest owners is brought about by the makeup of these boards, since 2 of their 3 members are chosen by local self-governing bodies in which the farming population is well represented. The third member is appointed by the government. The local representation on the county forestry boards insures that self-government is maintained. This ties in logically with the boards' main task of encouraging the initiative and self-activity of the small forest owner in the rational management of his forest. It also facilitates adaptation to local conditions. For a long period the county forestry boards were the sole agency for implementing forest policy. Not until 1941 was a central Private Forestry Board established, to obtain greater uniformity in application of the forest law, and to handle additional tasks such as training of forest workers, instruction courses for personnel of the county boards, and providing for impartial scaling of forest products and the procurement of good seed.

Educational and Advisory Work

Since educational and advisory work is considered the most important aspect of a constructive forest policy, it occupies most of the time spent by employees of the various boards and organizations.

In Sweden most of the educational and advisory work is carried out by the county forestry boards. Marking timber for cutting is a major activity; in fact, most of the timber cut for sale on farmers' woodlots, 25 million acres in total, is marked by county board employees. Other advisory work includes the supervision of sowing and planting, giving advice on silviculture and management, and preparing simple working plans and plans for roadbuilding and draining of swamplands. The forest owners are charged for individual service by employees of the county forestry boards, after a limited amount of free service.

The education of forest owners is another important function, and every county board has a demonstration forest with well-equipped buildings for this purpose.

Direct enforcement of the forest regulations occupies only a small portion of the time of county forestry board employees.

In Norway and Finland, educational and advisory work is no less developed, although it differs somewhat in details of administration, etc. The report states that "Sweden's experience strongly indicates that general forestry educational and extension efforts in the United States should be redoubled."

Grants-In-Aid

The grants-in-aid system is important in ensuring the performance of noncompulsory measures, as the grants tend to increase the yield of the forest by putting unproductive and idle land into production, e.g., by drainage of swampy land. Although the total amount of such subsidies is not great, it serves to induce a steady amount of amelioration work that otherwise would not be done.

The author says that a system of grants-in-aid deserves consideration in a comprehensive forestry program.

Forest Laws

The forest laws of the three Nordic countries have in common the fundamental aim of securing a sustained yield from the forests. Of interest here is the fact that sustained yield is by no means a new concept in the forest policy of Scandinavia and Finland. Especially in Sweden the large consumption of wood and charcoal by the iron industry in earlier times prompted far-reaching regulations to secure the future supply of wood for this industry. Before the use of coke, Sweden was the foremost supplier of iron to the world's markets (40 percent of world exports in the middle of the 18th century). Sustained yield was then secured by regulating the capacity and output of the iron industry, and later also of the growing lumber industry. Although this long period of government regulations in the last half of the 19th century was followed by a

liberal epoch, which eventually resulted in entire freedom in the use of forests as in other lines of national economy, it still represents the ideological and historical background against which the present forest policy should be considered.

The forest laws of all the three Nordic countries have two basic elements which are essential to sustained yield. The first is regulation to secure regrowth after cutting. This was followed by statutes to prohibit the cutting of young and still vigorous forests except by rational thinning. These regulations are made effective by different means in the three countries.

The forest laws of both Norway and Finland state that proposed felling of coniferous timber for sale or industrial use must be reported a specified time in advance of marking to the local forestry board, together with relevant information about the proposed cutting. Thus the board has an opportunity to impose specific requirements and instructions, if deemed necessary, in granting permission to cut.

The Swedish forestry law of 1905, amended in 1923 and 1948, is remarkable in so far as it represents the only existing forestry law that has stated the economic principle as the guiding one of management. However, the application of this principle has proved rather difficult, from both practical and theoretical viewpoints. According to rules laid down by the Private Forestry Board, the maximum expenditure required from the forest owner to secure "satisfactory regeneration within reasonable time" is to be calculated at an interest rate of 2½ percent. The same authority has set 3 percent as the interest rate for calculating the time when a stand is no longer considered vigorous and thus may be cut in ways other than by thinning. Obviously these interest rates are below that at which the forest owner may safely invest his money and still more below the rate at which he may borrow money. However, the interest rates thus prescribed correspond to the investments needed to secure regrowth even on poor sites and to maintain a rotation consistent with those already practiced in forests considered well managed. Unfortunately it has been shown that this application of the old formula of soil value does not give the results desired. The principal reason for this is that the formula considers only the isolated stand and neglects all the surrounding conditions that need to be considered by the owner—whether the state, forest industry, or farmer. For the same reason the formula does not give the results from the standpoint of the national economy that the low interest rates prescribed were intended to secure. However, these and other rules of application, issued by the Private Forestry Board, were only meant to be tentative and to serve as a guide.

Although the economic principle (judged from a national point of view) should control in the formulation of a forest law, its application evidently must be more flexible than it has been in Sweden. Some flexibility has been exercised in the application of the forest law, for the local forestry boards have continued to be guided by their sound judgment rather than by formulas. Incidentally, this may indicate the value of cooperation with the representatives of the forest owners in executing a policy. It proves further that there are limits to the degree of detail that is advisable in forest regulations, and also that forests must be regarded as a part of the complicated economic life that must ultimately be directed by the parties — whether communities, economic bodies, or individuals —that are responsible for the economic result.

It is interesting to compare the method by which Norway has administered compulsory regeneration after cutting. According to the Norwegian forest law of 1932, any person felling timber for sale or industrial use must deposit in a prescribed bank 2 percent of its gross value (i. e., at point of delivery or, if sold on the stump, 2 percent of the stumpage price increased 75 percent) to cover the cost of regeneration measures. The parish forestry board keeps individual accounts, and deposits are refunded to the owners as the regeneration measures are carried out. If inspection proves that no regeneration work is necessary, the money is simply repaid to the owner.

This arrangement has proved satisfactory in Norway. In a simple and practical way, it solves the question of financing regeneration, which is the crucial point in forestry.

In Finland also, regeneration is compulsory after cutting. For example, if a forest has been cut in such a manner as to jeopardize

natural regeneration, measures to ensure artificial regeneration are put in charge of the district forestry board, which may entrust them to the landowner. The owner must pay the cost unless the damage was done by another person from whom it is collectible.

The Farm Forest and Forest Policy

In evaluating Sweden's experience the author begins by stating that its circumstances are such that "nationally satisfactory forestry might be expected to result from individual and collective self-interest without public regulation. Forestry is profitable to private owners, large and small. Good forestry is practiced on public and company forests pretty much as a matter of course." Thus the main reason for a comprehensive forestry policy, as described above, is the farm forests. They comprise one-half—the best half—of the total forest area of Sweden.

What the author has said about Sweden will also be true in principle about Norway and Finland. The point that forestry is profitable to the private owner in Sweden (and Norway and Finland) is of course very important. Undoubtedly it helps greatly in realizing a constructive national forest policy.

The observation that forestry is a profitable business in Sweden is right in principle. However, as in agriculture, there are marginal lands in forestry where profitable applications of silvicultural measures are so restricted by the combination of poor soil or northerly location and bad marketing conditions that a satisfactory stand can not be secured after cutting. This is especially true in some forest types with poor conditions for natural regeneration, which for the most part are found at high altitudes in northern Sweden. It is a good thing that the state owns the greater part of these marginal forest lands and can thus manage them for the common welfare.

Just as there are marginal forest lands, there are also marginal forest owners. Not all of these are among the small forest owners. But, on the other hand, the small owner—he may be a farmer or not—does not have the same long-range attitude toward forestry as does the state or even the modern integrated forest industries with much capital invested in their mills. This capital leads the owner to use good forestry practices on his own land to safeguard his investments. This has proved true in Sweden, Norway, Finland, and other parts of the world.

The small forest owners also have a disadvantage because they cannot afford to employ trained forest personnel except by cooperation of some kind. The educational and advisory service of the forestry boards and cooperative societies cannot wholly eliminate this disadvantage. Yet this service has been a deciding factor in the modern forest policy of Scandinavia and Finland in securing fairly good management of the farm forests. Thus, the second forest inventory in Sweden (1938-51) shows that the stand of timber per acre in farm forests is only slightly less than that in company forests, considering the differences in site class. Statistics on the extent of certain silvicultural measures (sowing, planting, thinning) in forests belonging to the state, to companies, and to other private owners, mainly farmers, shows a certain lag in the case of the farm forests. However, representatives of the farmers have disagreed that there really is a lag.

It may be said that the forest policy of Scandinavia and Finland has been fairly successful. One of the reasons for this good result, not hitherto mentioned, is the far-reaching cooperation among the small forest owners in these countries.

Cooperation Among Forest Owners

The report gives special attention to different forms of cooperation among small forest owners. This cooperation has been highly developed in Scandinavia and in Finland. It may be regarded as an application to forestry of the extensive cooperation among the farmers in the sale and distribution of other farm products.

The object and activities of the forest owners' associations differ somewhat in the three Nordic countries. The forest owners' associations in Sweden have the widest range of activities, and about half of the privately owned forest land belongs to the association members.

These associations negotiate the price of forest products (pulpwood and saw logs) with the forest industries. They contract to supply large volumes to the industries and then fill these contracts by pooling the small volumes produced by their individual members. This solves the problem of marketing small quantities of forest products and at the same time

secures the best price possible to the forest owners.

In Sweden especially these associations have developed new lines of activities. Thus they put emphasis on helping their members to get the best net value from the timber cut. Each tree is carefully studied as to size and quality, to decide the most profitable way to cut it into saw logs and pulpwood. Attention is also given to the rationalization of logging. Latest models of tools and motor-saws are introduced, and members have an opportunity to rent heavy tractors, roadbuilding machines, and barking machines purchased by the associations.

In Sweden the forest owners' associations have also bought or built forest industries of their own. The primary reason for this activity is to regulate the price of roundwood sold by the members, especially through offering an outlet for roundwood that could not otherwise be marketed to advantage. However, a more recent motive seems to be that of enjoying the profit earned in processing the timber into lumber, pulp, and paper. As the latest development, a 60,000-ton sulphate mill has been built in southern Sweden through the joint cooperation of all the forest owners' associations. However, as the associations acquire more mills, they are increasingly in the position of being both buyers and sellers of roundwood, and they tend to pay their own members no more for roundwood than is necessary to ensure a reasonable profit.

The Swedish forest owners' associations have gradually extended their efforts to get their members interested in good forest management, and for this purpose have established good cooperative relations with the county forestry boards.

In his conclusion regarding forest owners' associations, the author says: "The situation in Sweden strengthens my conviction that there is a large need and opportunity for cooperative associations of small forest owners in the United States. While the conditions are somewhat different, I believe such associations can be of great service in collective marketing, operating wood-using plants, and promoting forestry—as they are in Sweden. The problem of efficiently marketing small quantities of timber, so vital to good forestry on small properties, has not been solved in America."

Outlook for the Future

Even admitting the fairly good results obtained through a forest policy, aided by other favorable agencies and advantageous natural, economic, and social conditions, the present state of forestry is not considered satisfactory in Sweden, in Norway, or in Finland. Evidence of this is given by the forest inventories of the three countries.

With the agencies now at work in the northern countries, a continued improvement of the forestry situation is assured, as the author says. It is equally true that forest inventories repeated at intervals have shown an increase in volume of standing timber and growth—in some instances a remarkable increase. Nevertheless, the present growth in Sweden represents only about 73 percent of the maximum growth theoretically possible. Although there must always be a gap between theoretical capacity and practical forestry, this gap is altogether too large.

Some of the causes of the shortcoming will cease to exist as time goes on—such as the unfavorable age class distribution in northern Sweden. But the narrowing of the gap will depend largely upon continued efforts of the public as well as the forest owners.

Forest research represents one aspect of this continued effort. Great consideration is being given to research in the northern countries, and especially has tree breeding caught the imagination as a means to increase the rather slow growth in these countries. The report deals with this and with several other sidelines of forestry that are impossible to cover in this review.

There is no better way to follow progress in your work than to make an inventory of the result. Thus, national forest inventories were first devised and tried in the Nordic countries. The first tentative inventory was in Värmland County, Sweden, in 1911. National forest inventories have been the most useful guides to forest policy in Scandinavia and Finand, and have helped more than any other agency to develop in the whole nation a living interest in forestry.

The Larch Sawfly in the Lake States

BY
SAMUEL A. GRAHAM

TAMARACK, eastern larch, or *Larix laricina* (Du Roi), K. Koch, has throughout its range suffered repeated defoliation by the larch sawfly *Pristiphora erichsonii* Htg. The earliest reports of this insect in North America are from New England and eastern Canada, 1880 to 1883. In the Lake States the first recorded heavy defoliations occurred in Michigan between 1906 and 1912 and in Minnesota between 1908 and 1914. Ruggles (1910) indicates that the insect may have been active in Minnesota as early as 1906 or 1907.

The sawfly population increased again in northern Michigan about 1917 and in Minnesota beginning in 1919, reaching a peak in 1926 and 1927. About the same time it became injurious in Northern Ontario. Some (Hewitt, 1912) have assumed that the larch sawfly was accidentally introduced into North America from Europe shortly before 1880 and that it spread westward from the Atlantic seaboard reaching Minnesota early in the twentieth century and northern Saskatchewan prior to 1915. This assumption may or may not be true (Coppl and Leius, 1955). However, some evidence indicates earlier periods of defoliation than those reported. Certainly prior to 1880 tamaracks in the Lake States had been repeatedly defoliated by some agency which produced an annual ring pattern very similar to that caused by known larch sawfly defoliation. These periods of reduced growth, that occurred from time to time throughout the life of the oldest trees that have been examined, will be discussed under effect of defoliation on ring width.

Even in 1910, before the extensive merchantable stands had been killed, it was unusual to find tamaracks in the Lake States older than 100 years. Since there is no reason to suppose that trees of this species are naturally so short-lived, the suspicion seems justified that some general catastrophe, late in the eighteenth or early nineteenth century, destroyed most of the large tamarack living at that time. There is evidence which will be presented later that such a catastrophe did occur between 1780 and 1800, and was caused by defoliation. The evidence suggests that the larch sawfly is native to North America.

This report on the larch sawfly is based upon many years of observation and experiment. The first observations were made under the direction of the late Arthur G. Ruggles in 1913 and 1914 in Itasca Park, Minnesota. During those seasons records were made of the seasonal activities of the insect, and cocoon collections were examined for the presence of the parasitic fungus *Isaria farinosa*.

Prof. Graham is at the School of Natural Resources, University of Michigan, Ann Arbor, Mich. In this investigation of the larch sawfly, Mr. L. W. Orr served as research assistant, contributing materially to the project. Through the later years, 1930 through 1934, the studies in Minnesota were continued by him alone. Acknowledgment is due him for the important part he played in the project.

Beginning in 1920 the study of this insect was reactivated in and near Itasca Park, Minnesota. In 1925 sample plots were established on which detailed records were kept through 1932. During the same period rearing and feeding experiments were conducted at the Itasca Park station of the University of Minnesota in cooperation with the then Bureau of Entomology, U. S. Department of Agriculture.

In the autumn of 1927 a study of larch sawfly and larch case bearer was begun in Mud Lake Swamp near Ann Arbor, Michigan. This was continued until 1932 when a fire destroyed the major part of the tamarack type in that swamp. Then followed the drought of 1934 to 1936 inclusive, during which time the sawfly population was reduced almost to the vanishing point throughout the Lake States. Thus the intensive study of the insect was halted before it could be brought to completion.

Since 1934 the sawfly has rarely been abundant in Michigan and then only locally. However, during 1950, occasional colonies were observed, and in 1954 the insect was present in small numbers in practically every tamarack swamp in northern Michigan. During 1955 an area of heavy defoliation was reported from the western tip of the State. Meantime it had reached outbreak proportions in parts of Minnesota, parts of Wisconsin and central Canada, where United States and Canadian entomologists are conducting intensive investigations.

This paper is intended to present information about the sawfly that was collected in connection with previous outbreaks in the hope it may be of value to those currently engaged in studying the insect. Conditions existing at the time of the previous outbreaks will be described, conditions that are definitely different from those common today. No attempt will be made to discuss the current studies although reference may be made to some of the published results that seem especially pertinent to the point under consideration. Reference to the selected bibliography will guide the reader to pertinent current literature such as Beckwith, 1954; Bird, 1955; Buchner, 1955; Drooz, 1953; Lejeune, 1951; and MacLeod and Heimpel, 1955.

Silvical Habits of Tamarack

Tamarack, one of the few deciduous conifers, is a highly intolerant species that invades wet lands ahead of other trees. At first it forms scattered pure stands on the areas invaded. Later, through continued invasion, the stands may become dense, sometimes numbering several thousand trees per acre. Often, if the tamarack stand remains relatively open, black spruce or, on seepages, white spruce and balsam fir may become established early and grow in mixture with the tamarack. In denser stands the invasion of the other species is slower, but by the time tamarack has reached large pole size, it will almost invariably have become mixed with an understory of other conifers, hardwoods, or both. These will ultimately replace it. Because of its high degree of intolerance, tamarack cannot become established under shade. Therefore, it seldom succeeds itself, and only one generation is likely to occur on the same area.

Tamarack ordinarily grows under two distinctly different environmental conditions, namely, on stagant bogs and on seepages. The first condition is characterized by a floating mat of vegetation that gradually thickens and ultimately becomes anchored to the bottom of a filling lake or pond. The second is characterized by a growth of bog plants, particularly sphagnum, sedges, and shrubs of the heath family, on soil kept wet by seepage water, usually from springs. Duncan (1954) reports that greatest establishment success occurs naturally on compacted moss, especially sphagnum, and where a continuous supply of moisture is available throughout the summer. Such conditions are most frequent in recently anchored or nearly anchored bogs and on carex and sphagnum covered seepages.

The floating bogs are invaded by tamarack about the time the mat becomes anchored to the bottom, whereas on seepages invasion follows the formation of the sphagnum-sedge mat over the wet soil. Thus both on bogs and seepages, tamarack usually constitutes the earliest tree stage.

Tamarack grows far more rapidly and attains larger dimensions on the upland than in the swamps. Trees three inches in diameter at ten years of age are not infrequent in such favorable locations, but in the Lake States the establishment of tamarack on high ground is rare. It is apparent that tamarack is a swamp tree not because it prefers that habitat, but, being a poor competitor, it is forced into the bogs and sphagnum covered seepages where other species cannot grow well.

Tamarack seed production is erratic, and although some seed is produced almost every year, heavy seed years occur rarely. As a result, the invasion of new areas is usually a relatively slow process extending over a period of from ten to twenty years. Once established the seedlings grow rapidly, however, often reaching a height of six inches or more during the first season provided they are growing in full sunlight.

After establishment the young tamaracks rapidly convert the open bog to a swamp forest. The growth of sphagnum immediately beneath the tree crowns is inhibited by shade, but between the trees the mat plants continue to grow vigorously, building up mounds of sphagnum.

As the trees increase in size and cast more and more shade, the mat which was originally continuous shrinks away from the root collars of the trees and becomes broken, with great hummocks interspersed with water filled depressions—a condition rarely encountered today but common in 1910. The tops of the hummocks at this stage are well above the general high-water level, but their sponge-like character permits water to be held and drawn from below by capillarity. Thus the mounds are maintained in a moist condition and, except during periods of severe drought, provide ideal cocooning locations for the sawfly. It was in swamps that had reached this stage of development that the greatest damage occurred during the 1908 outbreak in Minnesota.

Much of interest can be learned from the growth rings of tamarack. One very striking feature is that the reduction in radial growth rate characteristic of approaching maturity has never been observed in the present study. Individual trees exhibit reduced growth as a result of suppression, unfavorable weather, and defoliation but not from advancing age. This leads to the conclusion that the tamarack killed around 1910 was still in a vigorous condition when attacked and had not reached maturity.

Effect of Defoliation on Ring Width

The amount of woody growth of tamarack, as in any tree, is directly proportional to the amount of active photosynthethic tissue. Conversely, loss of foliage will result in a reduction of growth proportional to the foliage loss (Graham, 1931). Individual tamaracks seem able to withstand an almost unbelievable amount of defoliation without succumbing. Occasional trees may have their crowns almost completely killed and still survive by producing foliage from adventitious buds developing on the upper part of the main stem. Later such trees, in the absence of further defoliation, may reconstruct new crowns and recover.

Gross examination of the annual rings of such severely defoliated trees reveals that during the period of minimum foliage incomplete rings are apparently formed. These are, of course, very fine and disappear when traced around the circumference of the cross section. Thus it is very difficult to determine, from the rings alone, the exact age of such trees, or the years when defoliation occurred.

In 1953 one of these severely damaged but still living trees was located in northern Michigan and disks for detailed study were

taken at stump height. Because it was more than 200 years old, much older than most tamaracks that have been observed, it afforded an unusual opportunity to date previous periods of defoliation from the ring pattern if the correct date of a ring inside the band of slow growth could be determined. This tree grew in a locality where the first year of defoliation was reported by early records to have been 1906. This date was vertified by ring examination of less severely injured trees that had survived the outbreak. Such dating is, of course, subject to some error because all trees in a stand are not always heavily defoliated in the same season and, until it is almost complete, the effects of defoliation are difficult to recognize in the growth pattern. Therefore, the tree from which the sections were taken might have suffered the first severe defoliation in 1905, 1906, or 1907.

The first year of heavy defoliation of tamarack is usually marked by a narrow ring near the top, and at the base of the trunk by a ring somewhat wider than adjacent rings. Such a basal ring appeared in the specimen referred to and provided an approximate reference point. Because the top of the tree had been killed, the narrow ring near the top could not be dated.

After several fruitless attempts, using conventional procedures, to count the extremely narrow rings laid down during the period when the tree was virtually without living crown, a method was developed with the aid of Stephen B. Preston that made it possible to distinguish not only the bands of spring and summer wood but also to see individual cells. A thoroughly seasoned half disk from the base of the trunk was smoothed on a coarse sanding band and polished on a very fine band. A thin slice was then cut from the polished side using a band saw. Over a segment of the piece, including a part of the disk where minimum growth rate occurred, a long glass cover slip was mounted on Canada balsam. With relatively low magnification and strong transmitted light, it was possible to distinguish the cellular structure, especially in the thick-walled late wood. These cells stood out in sharp contrast to the thin-walled cells of the early wood.

An attempt was then made to count the annual rings through the period of slow growth back to the ring that had been tentatively identified as the one laid down in 1906. Most of the rings were clear, even though some consisted of only three rows of cells, two of thin-walled spring wood, and a single one of summer wood. In one part of the band five definite rings were included in the radial distance of 0.1 mm. Between the outer 1953 ring and that one designated as 1906, only one ring was not recognized.

Apparently during this uncounted season either the cambium at the point examined failed entirely to proliferate or only early wood was laid down. In the case of the two indefinite rings, the scattered heavy walled cells were lined up so that they seemed clearly part of a ring. Such scattered heavy walled cells apparently mark the point at which proliferation during one season was separated from that of the next.

Although the ring count was not accurate to the ring, it did at least prove that the assumed date for the ring designated as 1906 could not be in error by more than a year. Further vertification came from cross dating with sections from other trees an earlier defoliation pattern which began in 1877 that had previously been dated accurately.

History of Defoliation in the Lake States

The ring pattern in numerous trees growing in Iron and Gogebic counties, Michigan, shows clearly that defoliation became generally severe in 1906 and continued to about 1913. The minor outbreak which began in Michigan in 1917 and continued to 1929 can be identified by the rings.

Likewise the earlier period of severe defoliation mentioned above that started in 1877 and continued to 1885 can be recognized in the cross sections of surviving trees.

Because the great majority of trees surviving the severe defoliations of 1887 and 1906 were young at the time of the injury earlier defoliations can not be dated from them. Although ring patterns characteristic of defoliation injury are evident in the rings of all dead and fallen trees that were killed in the 1906-13 outbreak, the periods can not be dated without an identifiable reference point.

The tree discussed in the previous section, being over 200 years old, provided an unusual opportunity to date, at least approximately, all periods during the life of this tree that appear to have been caused by defoliation. Simultaneously retarded growth rates do not appear in the cross sections of hardwoods or most other conifers in the same locality. However, balsam fir and white spruce also suffered defoliation around 1880. Although defoliation could have been caused by some other insect, it is strongly suspected that the larch sawfly was responsible for defoliating the tamarack. Defoliation of fir and spruce was almost certainly caused by the spruce budworm, occurring simultaneously with the suspected sawfly outbreak.

In the following listing the periods are shown when defoliation apparently occurred during the life of this single tree. Question marks following the dates for a period of reduced growth indicate that in those instances the cause might have been either weather or defoliation. The periods of defoliation are for a single tree 230 years old.

1917 to 1929 incl.	1819 to 1823 incl.?
1906 to 1913 incl.	1791 to 1799 incl.
1877 to 1885 incl.	1781 to 1786 incl.
1864 to 1867 incl.	1752 to 1754 incl.?
1849 to 1854 incl.	1745 to 1749 incl.
1835 to 1841 incl.	1734 to 1741 incl.

This tree was a seedling in 1719 and showed no sign of defoliation injury until 1734, when it was 15 years old and approximately 1 inch in diameter. Thereafter repeated periods followed but were of relatively brief duration and caused light damage beyond a temporary reduction in growth rate. Not until 1781 did an outbreak occur which might have been comparable with the one that began in 1906. Then two periods of defoliation separated only by four seasons covered almost twenty years, 1781 to 1799 inclusive. It was about that time that most of the tamaracks killed around 1910 were seedlings or saplings. From this it appears that the life of a tamarack tree is characterized by a series of defoliation periods, most of short duration or moderate intensity. Only at long intervals may a disatrous outbreak be expected.

Information is at present unavailable to permit accurate determination of Minnesota outbreaks antedating 1908, but cross sections from old tamaracks show periodic defoliation similar to those for Michigan. But, although minor outbreaks do not necessarily occur simultaneously in different places, it seems likely that the disastrous outbreaks probably are influenced by conditions common to most localities in a region and therefore would be likely to develop almost simultaneously in an entire region within which similar climatic conditions prevail.

Following the 1908-14 devastating outbreak in Minnesota, there were six years when the sawflies were not numerous. Then the population increased again in the stands that had survived the earlier defoliation, younger trees for the most part. In Michigan a similar increase occurred in 1917.

Counts of twisted twigs, resulting from sawfly oviposition on four trees 15 to 20 feet tall felled in Itasca Park in 1923 indicate the trend in sawfly population between 1917 and 1923.

TABLE 1. Total and number of twisted twigs per tree.

Tree No.	1917	1918	1919	1920	1921	1922	1923
1	0	0	21	16	48	30	20
2	0	3	20	20	50	67	45
3	1	1	6	4	7	14	12
4	0	6	36	92	171	273	120
Total	1	10	83	132	276	384	197

Table 1 shows considerable variation between the number of twisted twigs per individual tree. This is to be expected because observations made during the early stages of any insect outbreak almost invariably show that certain trees are attacked a year or two before infestation becomes general.

The counts presented in Table 1 were made by examining all of the branches on felled trees. Each node on every branch was carefully examined for evidence of twisting for each year between 1917 and 1923. In most instances the nodes for each year could be recognized, but in case of doubt a cut was made and the annual rings counted in order to date a twist accurately. The trends are so clear from even the small number of trees counted that there was obviously a marked upswing in population numbers of the sawfly in 1918 in Itasca Park, and in 1919 defoliation on the trees examined was heavy. These data verify general observations that defoliation became conspicuous in 1919.

In 1924, 1925, and 1926, sample counts of twisted tips, on individual trees were made at various points in and near Itasca Park. Shoots were counted in groups of ten until the average ceased to change materially with addition of more samples. The most conspicuous characteristic of these counts was their variability from tree to tree and from place to place. In all 21,000 tips were examined in 1924 and about 35,000 were counted during 1925 and in 1926. During the three years there was clearly an upward population trend, indicated by the proportion of twisted tips. In Table 2, is shown the variations in the percentage of twisted tips from tree to tree and place to place during the three seasons.

At Fish Hook Lake the infestation was very heavy and uniform. There the percentage of twisted tips is indicated by a single figure for each season. For other localities, the figures represent the most heavily and most lightly infested tree observed at each point for each of the three seasons.

TABLE 2. Range in percentage of twisted tips per tree in and near Itasca Park.

Locality	1924	1925	1926
Floating Bog	2 –8	1–14	1–25
Fish Hook Lake	22	20	35
Becida Swamp	12–13	5– 8	2–15
W. of Lake Itasca	1– 4	3– 4	4– 8

21,000 tips examined in 1924.
35,000 tips examined in 1925 and 1926.

Beginning in 1925 the abundance of the sawfly was measured in terms of average amount of defoliation occurring on a series of 20 one-chain-square sample plots (1/10 acre). In 1928 the number of plots was increased to 23, three plots in Iron Spring swamp being added that year. In 1931 two more were laid out near Charissa, Minnesota, where a relatively heavy infestation seemed to be building up. The amount of defoliation was expressed in percentage classes, as a *defoliation index*, as follows:

0 = none
1 = less than 1 percent
2 = 1–19 percent
3 = 20–39 percent
4 = 40–59 percent
5 = 60–79 percent
6 = 80–99 percent
7 = 100 percent

These records overlap by two years the observations based on twisted tips and to a certain degree indicate the relation between the two procedures. The sharp reduction in sawfly damage that occurred in and near Itasca Park during 1929 and 1930 (Table 3) is conspicuous, being less than 20 percent on all plots and amounting to only a trace on most plots. In contrast, one of the plots near Clarissa, no. 24, that had suffered little defoliation prior to 1930, was heavily defoliated in 1931. In following seasons the infestation on the Clarissa plots declined rapidly.

After 1930 the sawfly population declined so that it was pointless to continue annual examination of the plots in and near Itasca Park. Observations were continued at Clarissa through 1932. In some other localities the sawfly continued to be numerous in certain swamps through 1935, even though the general population over the Lake States declined.

The defoliation on the 20 plots established in 1925 (Table 3) reached a peak in 1926, declined slightly in 1927, was conspicuously less in 1928, and dropped to an inconsequential amount in 1929.

TABLE 3. Average defoliation index on sample plots.

Plot No.	No. Living Trees	Ave. DBH	1925	1926	1927	1928	1929	1930	1931	1932
1	0	7.2	Few survivors of 1909-13 outbreak killed by '25							
2	3	9.6	4	--	7	5	3	1	--	--
3	47	3.9	4	6	6	4	1	1	--	--
4	10	7.2	4	6	6	4	1	1	--	--
5	31	4.8	4	7	6	3	1	2	--	--
6	27	4.7	3	7	5	3	1	1	--	--
7	19	5.1	5	7	7	2	1	2	--	--
8	67	4.2	3	7	6	3	1	1	--	--
9	196	2.0	4	7	7	2	1	1	--	--
10	64	2.3	2	5	4	3	1	1	--	--
11	206	1.0	2	4	5	2	1	1	--	--
12	97	1.4	2	6	3	2	1	1	--	--
13	58	3.9	4	7	7	4	1	2	--	--
14	9	5.9	2	7	0	1	0	1	--	--
15	11	7.6	6	7	7	2	2	2	--	--
16	224	1.6	3	7	6	2	1	1	--	--
17	294	1.2	2	5	2	2	1	1	--	--
18	3	5.1	0	0	0	3	1	0	--	--
19	188	2.4	3	7	4	2	1	1	--	--
20	18	4.7	4	7	7	2	1	2	--	--
21	80	2.8	--	--	--	4	1	1	--	--
22	125	1.4	--	--	--	4	1	1	--	--
23	43	3.4	--	--	--	4	1	1	--	--
24	1	6.9	--	--	--	--	--	--	6	3
25	80	3.0	--	--	--	--	--	--	2	2

TABLE 4. Mortality of tamarack associated with defoliation.

Plot No.	Initial No. tamarack	Ave. DBH	Killed 1908-14 no.	Killed 1908-14 percent	No. living 1925	Dying 1925-30 no.	Dying 1925-30 percent	Vigor Rating[1] 1925	Vigor Rating[1] 1928
2	240	9.6	180	75	30	10	33	2.0	1.3
15	180	7.6	70	39	110	30[3]	27	2.2	1.6
1	130	7.2	130	100	0	0	0	D	D
4	200	7.2	100	50	100	50	50	2.8	1.5
14	360	5.9	270	75	90	80	90	2.0	2.0
7	520	5.1	330	63	190	80	42	2.4	0.4
18	420	5.1	390	93	30	0	0	2.3	2.3
5	530	4.8	220	42	310	0	0	2.5	1.7
6	530	4.7	250	47	270	170	63	2.1	0.6
20	450	4.7	270	60	180	0	0	2.2	2.0
8	850	4.2	180	21	670	70	10	2.5	2.5
23	760	3.9	290	38	470	30	6	2.6	2.4
3	760	3.9	180	24	580	30	5	2.5	3.0
13	1,910	2.4	0	0	1,880	150[2]	8	2.0	2.0
21	720	2.3	80	11	640	40	6	2.8	2.7
19	2,170	2.0	210[2]	10	1,960	290[2]	15	2.3	1.8
10	2,290	1.6	40[2]	2	2,240	210[2]	9	2.1	2.2
9	1,050	1.4	80	8	970	30[4]	3	3.1	3.3
16	2,940	1.2	0	0	2,940	600[2]	20	2.4	3.0
12	2,090	1.0	0	0	2,060	62	3	2.4	2.9
22	800	3.4	370	46	430	40	9	----	2.5
17	1,290	2.8	490	38	800	0	0	----	2.4
11	1,250	1.4	0	0	1,250	50	4	----	3.1

[1]Vigor rating: D, dead; 1, very low; 2, low; 3, medium; 4, good; 5, very good.
[2]Mortality probably due chiefly to suppression but contributed to by defoliation.
[3]Dying, 1930.
[4]140 additional trees per acre girdled and killed by snowshoe hare.

Mortality of Defoliated Tamarack

The ability of tamarack to withstand severe defoliation has already been mentioned. However, in spite of this ability a tremendous amount of mortality occurred among the defoliated trees, especially during the 1908-1914 outbreak in Minnesota and that in 1906-1912 in Michigan. In general it was the larger trees that succumbed. Some of the results on the series of plots mentioned in the preceding section are presented in Table 4.

Prior to 1925, mortality due to defoliation was almost entirely the result of the older outbreak, 1908-1914. Between 1925 and 1930 the mortality was due to defoliation between 1919 and 1929. In the denser stands much mortality is probably attributable to competition, although contributed to by defoliation. Clearly the heaviest mortality during both outbreaks occurred on plots where the larger trees were growing. As a general rule, size classes over 5 inches D.B.H. suffered heavy mortality during both outbreaks, whereas trees under 3 inches suffered much less.

Development and Habits of the Sawfly

Emergence of the sawfly adults occurs in early summer and is synchronized with the normal time of expansion of the terminal buds of the host tree. These buds develop into shoots several inches in length with single needles arranged spirally. Lateral buds, on the other hand, produce a fascicle of many leaves, stem growth being limited to the addition of a terminal ring to the spur on which each bud is borne.

TABLE 5. Relation of numbers of eggs to terminal shoot length (Averages taken from smoothed curve).

Number of shoots observed		Length	Eggs per shoot				
			Maximum		Minimum		
1929	1930	in cm.	1929	1930	1929	1930	Average
0	1	1.5	0	15	0	15	15
18	9	2.0–2.9	24	12	5	14	16
49	77	3.0–3.9	29	26	9	12	19
53	18	4.0–4.9	34	36	6	11	23
39	10	5.0–5.9	38	39	8	13	27
30	5	6.0–6.9	50	41	5	13	31
16	3	7.0–7.9	65	37	11	30	35
16	1	8.0–8.9	44	39	10	39	39

Data for 1929 from Floating Bog and Iron Spring Swamps.
Data for 1930 from Floating Bog, Laporte, and Clarissa.

The sawfly eggs are deposited in a series of slits cut by the female's ovipositor along one side of an expanding terminal causing the twist in the shoot already discussed. The amount of twisting is correlated with the number of eggs deposited. In turn the number of eggs per shoot bears a direct relation to the length of the shoot.

The shortest shoot in which eggs were laid in 1929 was 2 centimeters long, but shoots were not favored under 3 centimeters. In 1930 a single shoot containing eggs under 2 cm. long was found. Although the average number of eggs increased with each length class, it seems unlikely that lengths above 6 or 7 centimeters would have an appreciable influence upon the number of eggs deposited per shoot.

The data presented in Table 5 for 1929 and 1930 are surprisingly similar, in spite of the fact that they were collected in a number of different swamps during two different seasons.

On hatching, the tiny, dark-headed, greenish larvae feed gregariously, usually beginning on the fascicle of leaves nearest the base of the shoot where the eggs were laid, and continuing on successive fascicles until the twig is completely defoliated. Then they move as a group to the nearest adjacent twig, defoliating that in the same way, and so on until they have completed their growth. Thus individual branches are defoliated while other parts of a lightly infested tree may remain untouched.

The data presented in Table 6 indicate clearly that the gregarious habit of feeding results in severe localized injury to the parts of the trees that have been defoliated. Also it appears that the size of fascicles on the tree as a whole is materially reduced by repeated defoliations. When adjacent branches were compared one defoliated and the other undefoliated during the previous season it was observed that in the case of every pair but one the fascicle weight was less for the previously defoliated than for the undefoliated branch. All the deviations are in the same direction. Comparing the branches undefoliated in the above series which came from trees partially defoliated for several years with trees growing in the nursery that had never been appreciably defoliated, and where the mean weight per fascicle was 0.029 gm., the difference in fascicle weight is conspicuous. A part, but not all, of this difference is accounted for by the more favorable site conditions in the nursery.

Two of the ten branches completely defoliated in 1928 died, one of them after leafing out in 1929. On a third branch the tip was killed. This mortality of in-

TABLE 6. Effect of defoliation on weight of tamarack fascicles in 1929.

Branches undefoliated 1928		Branches completely defoliated 1928	
No. of fascicles	Gms. dry wt. per fascicle	No. of fascicles	Gms. dry wt. per fascicle
265	.023	288	.018
105	.019	219	.016
125	.017	380	.017
418	.012	230	.008
176	.017	151	.010
118	.013	196	.010
164	.019	268	.008
159	.014	239	.010

dividual branches and tips explains why the crowns of repeatedly defoliated trees may become reduced until almost no living branches survive.

Now let us return to a consideration of the sawfly itself. On reaching full development, the larvae drop from the tree and burrow into the moss or litter until they find conditions of moisture favorable for pupating. On upland this usually means the surface layers of the litter-covered mineral soil. In the swamps the depth to a favorable location in the moss varies with weather and other conditions. Usually the larvae do not penetrate deeper than a few inches. However, during a drought the moss may become dry to a depth of eighteen inches or even two feet. Then the larvae usually will make their way downward to a moist sub-stratum or die. Sometimes after cocooning under too dry a situation they will die within the cocoon. In 1931 Orr observed in a swamp near Clarissa, Minnesota, where the larvae could not reach a moist spot to cocoon, that prepupae within apparently normal cocoons were dead and shriveled. The depth to which the larvae penetrate has an important practical influence upon the sawfly population as later flooding of dry swamps may drown those that have cocooned in the prepupal stage within the cocoon.

As with many other sawflies the dormant condition may continue for two years or longer. However, the majority will transform to pupae and adults the summer following cocooning, emerging in June to oviposit and begin another generation.

The proportion of prepupae that remained in diapause over a single winter and those that passed through two or more winters in a dormant condition was determined by a series of rearing experiments. The cocoons were placed in sphagnum moss in wire-screen cages that were set out in a swamp where they were exposed to approximately the same weather as if they had been uncaged. From these data it appears that more than 90 percent of the adults in these tests emerged the summer following cocooning, and four or five percent of the prepupae lived over two winters. Less than two percent passed the third winter in diapause. Results were consistent in this series of overwintering tests, the first started in 1924, and the others in 1925 and 1929 respectively. Emergence at the end of the first winter was 92, 92, and 96 percent respectively. After three winters 0.4, 0.2, and 0 percent of the prepupae which had not been killed by parasites or other causes were still alive within the cocoons.

The 1924 and 1925 experiments were conducted under a variety of conditions to determine those best suited for survival of the sawfly. High mortality of the cocooned insects occurred in the unfavorable situations where they were exposed to relatively dry and warm situations. The most favorable conditions for survival were under a covering of an inch or slightly more of moist sphagnum moss. The unusually high mortality in 1929 and 1930 was due largely to the dry and hot weather that prevailed during those years.

Although the larch sawfly is parthenogenetic, there are nevertheless a few males in the population. Mating of the sexes, however, was not observed, but probably does occur. The proportion of males varies

greatly from time to time and from locality to locality. During 1913 and 1914 only one male was obtained from an unrecorded number of cocoons, certainly less than one percent. Ruggles (1910) reported having reared 125 adults, of which three were males, and in the following year one percent in another lot of sawflies.

Between 1926 and 1930, however, rearings designed especially to determine the proportion of the sexes indicated a much larger proportion of males. The sex factor for individual lots of cocoons varied greatly. It has been suspected that at times there may be a differential mortality between the sexes, the males surviving under adverse conditions and the females succumbing in greater proportion. Although this may be a logical hypothesis, it is not supported by the facts observed in 1913 and 1914, when defoliation was so severe that a large proportion of the larval population must have experienced food shortage before cocooning. In spite of this, the proportion of males was lower then than in any of the later rearings in Minnesota. Smith (1955) discusses the cytogenetic potentialities and suggests that the action of high temperature may have an influence upon the number of males produced in any generation.

TABLE 7. Proportion of males and females.

Year	Number females	Number males	Total number	Percent females
1926	20	4	24	83
1927	133	11	144	93
1928	530	21	551	96
1929	63	4	67	94
1930	126	4	130	97

In Table 7 is shown the variations observed in the proportion of males and females at Itasca Park during five different seasons. This series of rearings was designed especially to determine the sex factor. All five seasons were relatively warm but 1929 and 1930 were both very hot and dry. The only conclusion that can safely be drawn from the information at hand is that the proportion of males varies, usually between one and four percent but occasionally may be considerably higher.

Seasonal History

Although the general pattern of development remains the same, the seasonal history of the sawfly varies somewhat from year to year. For example, in Itasca Park in 1914 and again in 1931 the adults were emerging by June 1. In 1929, however, the first adult was seen on June 6 and general emergence was delayed until after mid-June. In contrast, during 1914 few unopened cocoons could be found in the swamps on June 15, and oviposition was under way by that time. Similarly in 1929, although emergence was much later, oviposition began about the middle of June and was practically finished by June 25. In 1914 hatching was observed on June 22 and in 1929 the earliest eggs deposited began to hatch on June 19. Thus by the time of hatching the difference due to late emergence had been largely eliminated.

The first cocooning in 1914 was observed on July 24, no larvae remaining on the trees by August 3. In 1928 cocooning began about July 20 and continued until August 10, whereas in 1929 the larvae had all left the trees by July 24, some before completing development, as shown later. In 1929 there was clearly an acceleration of the developmental rate due to continuously warm, clear weather for 20 days in July. Similarly in 1931, also a warm season, Orr reported that cocooning was early, beginning on July 25.

As a rule in the general locality of Itasca Park, Minnesota, the seasonal history that may be expected is about as follows:

Emergence of adults	June 1 to 15
Oviposition	June 10 to 25
Larval stage	June 19 to July 31
Cocooning period	July 20 to Auugst 10

TABLE 8. Number of adult sawflies, exhibiting indicated reaction to temperatures.

Temperature in °C.	25	27	29	31	33	35	37	39	41	43
Inactive	1		1			1				
Very active	10	3								
Disturbed		7	6							
Highly disturbed		1	2	6	5	2				
Frantic			2	5	6	6	6	2		
Partly paralyzed						2	4	6	2	
Paralyzed							1	3	3	
No movement									6	

In the Upper Peninsula of Michigan each of the periods will be about 5 to 7 days later. For instance, in 1954 larvae were observed in Iron County after the middle of August. Near Ann Arbor emergence of adults occurs at least two weeks earlier than in Itasca Park, and because of the warmer climate cocooning usually begins by July 1.

Temperature Reactions of Adults

Observation of adult sawflies in the field indicates that there is little activity at temperatures below 19°C. Between 20° and 27°C, the females are active. During the period of rapid warming in early morning they respond to temperatures above 25°C by seeking shade. This is not true at midday, when oviposition may occur at about that temperature. In a single instance a female was seen laying eggs at 29° C, the highest at which normal activity was observed. When too warm, the sawfly adults burrow into the moss, where under ordinary conditions of moisture they can escape high temperature.

In order to test experimentally the temperature preferences of adult sawflies, seven females were placed on June 28, 1928, in a glass tube 1 by 39 inches with a gradient ranging from the temperature of ice at one end to that of steam at the other. From 4:45 P.M. until 5:25 P.M., the insects remained in a temperature range between 24° and 32°C. At 5:40 P.M. they moved toward the cool end, coming to rest between 21° and 25°. At 6:10 P.M. they were resting between 15° and 21°C. This experiment was not conducted on a scale sufficient to be conclusive, but combined with field observations it has significance. Both the experiment and field observations indicate that during the day the insects prefer warm places where the temperature is around 25° or 26°C, but at night select cooler situations.

In order to obtain some idea of the effects of high temperature upon the sawflies, a series of females was subjected to slowly-rising temperature until a fatal point was reached. After being cooled to a state of inactivity at 11°C they were permitted to warm slowly to 22°C, at which time they were normally active. They were then placed in a glass heating chamber equipped with a thermometer and the temperature was raised slowly. The results are summarized in Table 8.

The observations show clearly that sawfly adults are unable to endure extremely high temperature, succumbing after relatively short exposure to about 40°C. The results suggest that continued exposure to 35°C might prove fatal, since some individuals became partly paralyzed from short exposures to that temperature. Clearly the insects attempt to avoid conditions in excess of 29°C.

Temperature Reactions of the Larvae

No experiments were conducted to determine the reaction of larvae to tempera-

ture, although some colonies caged on branches in the sun with restricted air movement died, apparently from heat. It is reasonable to expect, therefore, that unusually hot weather might result in high mortality if it occurred during the larval period. Although no direct evidence of this was observed even in 1929, a season during which high temperatures occurred far more frequently than usual, indirect evidence pointed to temperature-caused mortality. Especially high temperature prevailed during the last few days that fully grown larvae were observed on the trees, i.e., on July 24, 25, and 26 when air temperatures of 30°C 36°C, and 39°C were recorded respectively in the weather shelter in the forest nursery at Itasca Park.

During these three days no larvae were actually observed in heat prostration, but their complete absence from the trees thereafter indicated that temperature probably stimulated them to drop from the trees sooner than otherwise might have been the case. Ruggles, (1910) observed a similar situation in 1910, a very dry, hot year, stating that the larvae left the trees before all the foliage had been consumed. The suspicion that high temperature caused the larvae to leave the trees early in 1929 is strengthened by the record of food consumed through the 5th instar in that year as compared with 1930: i.e., 0.170 grams per larva in 1929 and 0.265 grams per larva in 1930.

Seasonal Temperature in Moss

The reaction that prompts adult sawflies to seek shelter in the moss from excessive heat has previously been mentioned. During the summers of 1928, 1929, and 1930, temperature on the moss surface and at various depths was recorded daily in a number of locations. During one winter, observations were made from time to time. In addition, other temperature measurements were made in various locations at irregular intervals. As would be expected, the surface of the moss in tamarack swamps exhibits the greatest variability of temperature.

The maximum temperatures recorded occurred in full sunlight during 1929 when air temperature was close to 40°C and the surface of the moss was dry. Under ordinary conditions the surface temperature would have been much lower because of the cooling effect of evaporation from the moist moss. Similarly, the low sub-zero surface temperature of −14°C was very unusual, occurring during very cold winter weather when there was no blanket of snow covering the ground. Ordinarily winter temperature in the moss will be very little if any below the freezing point of water when the ground is covered with snow.

But even under the most extreme conditions found, the sawfly would not necessarily be subjected to temperatures beyond the limits of toleration, since winter temperature is never lower than −5°C at depths of one inch or more in the moss, and in summer either larvae or adults can usually find cool spots in the shade or in the moss where they are not subjected to excessive heat. In nature the insects can almost always find temperatures that are endurable, except when larvae are forced by high temperature to leave the trees before development is complete, or when cocoons are spun near the surface of dark-colored, decomposed peat.

Food Requirements of the Larvae

In 1928 an effort was made to determine the quantitative food requirements of individual larch sawfly larvae. Each larva was fed separately on individual twigs and an attempt was made to record the amount of food eaten in terms of numbers of needles or fascicles. Two difficulties were encountered. First, when feeding individually the larvae failed to consume completely either the individual needles or the fascicles upon which they fed, and secondly these naturally gregarious larvae did not appear

to eat normal amounts of foliage, many dying before development was complete.

In 1929 groups of larvae were fed together both in the laboratory and under natural conditions in the field. Every few days the larvae in each group were counted and their numbers recorded according to instars. Also the number of fascicles eaten during each period was recorded. The fascicles on the various branches varied considerably in size. In order to arrive at a reasonably satisfactory estimate of the fascicle size, the dry weight per fascicle on each branch was estimated individually by weighing the fascicles on an adjacent branch similar to the one on which the larvae were feeding. By multiplying this average dry weight per fascicle by the number of fascicles consumed an approximation of the foliage eaten expressed in grams of dry weight was obtained for each group of larvae. This study was repeated in 1930. The results demonstrated clearly that the greater proportion of defoliation occurs during the fourth and fifth instars. The total cumulative food consumed per larva in grams dry weight during 1930 was thus estimated to be 0.0003 through the first instar, 0.0034 through the second, 0.0150 through the third, 0.0625 through the fourth, and 0.0265 through the fifth.

Mention has previously been made of the lower consumption of food per larva during the 5th instar in 1929, 0.170 grams, presumably due to the fact that the larvae ceased eating and dropped from the trees sooner than normal because of the excessively hot weather on July 24, 25, and 26.

Reproductive Potential and Fecundity

The reproductive rate of the larch sawfly varies tremendously from individual to individual and from season to season. Beginning in 1927 an attempt was made to rear the insect in the insectary and, in doing so, to determine both its food requirement and its capacity to reproduce.

This undertaking proved to be more difficult than anticipated. Branches containing eggs in the new tips were placed in bottles of water in the insectary and the eggs were permitted to hatch. The larvae immediately started feeding gregariously on the nearest fascicles. Fresh foliage was provided almost daily. At first the fascicles on which the larvae were feeding were clipped off and placed on the fresh food with the larvae still thereon. Later, fresh branches were placed in contact with those on which the larvae were feeding so that they could conveniently move to fresh food.

Some were prompt in moving from old to new branches, whereas others refused to move immediately. Since fresh branches were available and it was assumed that the larvae would move from undesirable foliage promptly, this seemed to be of little importance at the time. However, in 1928, an unintentional experiment indicated otherwise. One lot, initially 231 larvae, through a misunderstanding were permitted to go without fresh food for a period of three days during the fourth instar. At the end of three days the leaves showed slight signs of fading and the larvae were not eating normally. Fresh foliage was supplied and the larvae fed until fully developed. The number cocooning from this lot was not recorded, but only 15 adult females emerged in the early summer of 1929 after passing the winter under natural conditions buried in moist sphagnum. These adults were dissected and the well-developed eggs in the ovaries counted. One was sterile, one contained 87 eggs. The average number was 40 per female, a number far below expectation.

This experience indicated that even a short period of starvation during the larval period can affect the number of eggs that a female sawfly will produce. Therefore, in rearing experiments, errors can easily be introduced inadvertently. In later feeding experiments care was exercised to see that the larvae were provided with fresh foliage, but even so it is suspected that varia-

tions in food quality might have affected the reproductive capacity of the females. Recently a thorough study on the effects of starvation during the fifth larval instar has been made by Heron (1955), substantiating the conclusion that fecundity of the sawfly is affected even by a brief period of hunger.

When the fecundity of females is determined by dissection the question arises as to when the eggs that will be deposited are all fully developed. A comparison was made of appparent fecundity and age of the adults reared from cocoons collected in the field. The data from the 18 dissections were too few to demonstrate conclusively that some of the smaller eggs contained in the oviducts grow to full size after emergence of the female from the cocoon; nevertheless, such development is indicated. A definite difference was observable in the appearance of the eggs between the newly emerged females and those 5 days old. There was a gradation from large to small eggs in the newly emerged specimens, whereas in the older individuals there was a recognizable difference between the larger eggs and those that would almost certainly fail to develop fully. Therefore, egg counts made in females several days old should be more accurate than those made earlier, and it seems likely that the correct number of eggs that could be deposited was underestimated in the case of the younger females.

A considerable number of females from known origin were dissected. Some were from larvae reared on trees growing in the nursery at Itasca Park. Others were from insectary-reared larvae, whereas others were from wild cocoons collected in tamarack swamps. The series derived from females that had had an opportunity to mate are indicated in Table 9 as mated females. Although the act of mating was not actually observed, the pairs were confined together during oviposition. Table 9 compares the distribution in fecundity classes of the dissected females from the various sources. Those from mated parents suffered the effects of malnutrition already discussed.

TABLE 9. Number of females in each fecundity class (53 dissections).

Number of eggs	Reared on nursery trees	Reared in insectary from Mated parents*	Unmated parents	From wild cocoons
0	0	1	0	0
1–20	0	2	0	0
21–40	0	7	1	0
41–80	1	4	6	10
81–100	2	1	4	7
101–120	0	0	1	5
120–140	0	0	1	1

*Lot inadequately nourished.

It is, of course, doubtful if any female will lay all the fully developed eggs in her body. In fact gravid females in some instances failed to oviposit at all . Four of these were dissected and found to contain 113, 130, 107, and 109 eggs respectively. Sixty females were dissected which had been given an opportunity to oviposit, and all had retained a surprisingly large number of eggs. The smallest number was 11 and the largest 127. Clearly the females refuse to oviposit unless they find conditions to their liking.

As part of the study of the oviposition habits of the larch sawfly, a series of newly emerged females were caged individually on tamarack branches, the first on June 5, and the last on June 26, 1928. The results are summarized in Table 10.

TABLE 10. Number of females in each oviposition class and date of emergence during 1928 season.

Number of eggs laid	June 5	6	9	10	12	16	20	21	24	26
0	0	8	2	0	0	0	0	0	0	0
1–10	0	2	0	6	0	3	1	1	0	0
11–20	2	0	2	0	4	2	3	3	0	2
21–40	0	0	0	0	3	2	4	4	1	0
41–80	0	0	0	3	0	1	3	3	1	0

A considerable proportion of females emerging prior to June 10, 1928, failed to deposit any eggs. Presumably this was because terminal growth had not developed sufficiently at that time to provide enough suitable places for oviposition when they were ready to deposit eggs. After June 10 all females observed deposited some eggs, and the maximum number laid per female was greater.

Dissection of females demonstrates that the failure to oviposit is not ordinarily due to sterility of the females. Furthermore, the positive relation between the number of eggs deposited and the length of the new terminal growth suggests that the actual number of eggs laid by a female depends not only upon the number of eggs matured, but even more upon the environmental conditions encountered during oviposition.

If we assume that all of the females dissected were subjected to some unfavorable conditions during their development, it seems probable that the number of eggs representing the potential fecundity of the species may not have been observed. However, it appears that the maximum number of eggs contained in the body of a female would closely approximate the number since in several instances it appeared that the abdomen could hold no more. The largest number observed was 130. Assuming a sex factor of 0.98 (98 percent female) the reproductive potential for the species would be 117 progeny per individual per year.

Causes of Mortality

Beginning in 1924 and continuing through 1934, studies were conducted to determine the causes of larch sawfly mortality that were influencing the population trends from year to year.

Egg counts were made and the number of eggs parasitized and failing to hatch for other reasons were recorded. Larval groups were watched through their development to see what predators or parasites were attacking them and how they were responding to the effects of their environment.

Larvae disappeared from the feeding groups for reasons that were obvious, but many were unaccounted for. Therefore, trays with wooden sides and cloth bottoms were set beneath the feeding groups so that any larvae falling from the branches would drop into the trays. They were prevented from leaving the trays by bands of tanglefoot. In later years moss was placed in the trays to give the larvae protection and a place to spin cocoons.

After the larvae reached full development they were permitted to form cocoons and these were planted in cages buried under natural conditions for sawfly hibernation in a tamarack swamp. These cages were watched for the emergence of adults and parasites. At a later time, usually the second fall after cocooning, the cocoons were counted and from their condition was determined the number from which adults had normally emerged, the number from which Ichneumon parasites had emerged, the number parasitized by small parasites, mostly Pteromalids, and the number dying from other causes. Thus at the end of each experiment the observed emergence was supplemented by this careful examination of the cocoons.

Observation made on the cocoons from which known types of insects had emerged made it possible to recognize from field collections of cocoons the influence of the various resistance factors operating during the cocoon stage in different swamps. Unfortunately, it was not possible, because of their durability, to recognize with certainty the age of cocoons collected under natural conditions. Thus any one collection might represent an accumulation over several years. Therefore, information obtained from such collections cannot be interpreted in annual terms.

The following sections will consider the various causes of mortality that have been observed to influence the larch sawfly populations in Minnesota and Michigan.

Heat

The influence of heat has already been discussed. Only during 1929 did temperatures occur that were sufficiently high to cause the larvae to drop from the trees before completing development, and this came so late in the season that many had already cocooned. It may be concluded that temperature is seldom a limiting factor in swamps covered with a growth of sphagnum moss. However, 35°C or higher during the larval stage could result in serious indirect injury to the larvae by forcing them to drop from the trees before they completed their growth.

In swamps that have been drained, where the peat has decomposed to a black, muck-like condition, the surface of the dark-colored soil may attain temperatures fatal to the larvae. Under such conditions larvae may be killed by heat when they drop from the trees to seek cocooning locations.

This phenomenon was observed in 1932. Success of cocooning in normal sphagnum cover and in black decayed peat was compared under the same tree. A layer of black peat several inches thick was spread over an area beneath the crown of a tamarack tree. This covered area was located on the south side where it was exposed to direct sunlight. The remaining area beneath the tree was sphagnum covered. Five hundred larvae in the third to the fifth instar were placed on the branches of this living tree above each of the two conditions. Numerous dead larvae were later observed on the surface of the muck. These had died before being able to burrow beneath the hot surface.

In the following spring 94 normal-appearing cocoons were found in the living sphagnum, adults had apparently emerged from another 10 cocoons, and 172 cocoons had been opened by mice. A few of these last might have been spun during a previous season. However, almost 300 were accounted for in the living sphagnum beneath the branches where 500 larvae had been placed. In the black muck 9 cocoons were found containing living larvae, 46 were shrunken and collapsed, and 11 were only partly formed. No evidence of mice was observed in the muck area. Both the muck and the sphagnum were moist so that the important variables were temperature and, of course, the physical structure of the two substrata.

Physical Structure

Preliminary studies by Orr indicated that the physical structure of the moss or peat where the larvae spin cocoons has an influence upon the cocoon stage. In certain drained and pastured swamps where the peat had decomposed to a black muck an unuually large number of thin, partially formed cocoons were found and an unusually small number of healthy prepupae were contained in the cocoons. In nature it was impossible to determine whether these conditions were due entirely to heat and dryness or whether the structure of the medium in which the larvae were forced to cocoon had an influence. Of 221 larvae presented under field conditions with the opportunity to spin in decomposed or partly decomposed peat, only 44 were successful in forming complete cocoons, 35 were partly formed. The other larvae died without spinning.

In order to test the hypothesis that the condition of the peat might be influential, larvae were placed in vials in the laboratory. Four of the vials contained moist decayed peat and two undecayed sphagnum. Of 14 larvae placed in the peat, only 8 formed normal cocoons and only 4 were found to contain live larvae. In contrast, all 8 of the larvae placed in the moss formed normal cocoons containing live larvae. These preliminary results strongly suggest that the character of the medium in which cocoons are formed influences the number of sawflies passing successfully through the cocoon stage. Why this should be is not clear.

To test the relative desirability of decayed peat and undecayed moss as an over-

wintering medium, normal cocoons were placed in four cages, two containing decayed peat and two undecayed moss. One of each was stored over winter in the unheated insectary, the other two under natural conditions in the swamp. Records of the number of cocoons used were burned in a fire that destroyed the Itasca laboratory in 1932 but the same number was placed in each cage. Table 11 shows the record of emergence in 1933.

TABLE 11. Emergence following overwintering in moss and decayed Peat.

	Unheated insectary		In Tamarack Swamp	
	peat Decayed	moss Undecayed	peat Decayed	moss Undecayed
Sawflies	2	27	8	22
Mesoleius	3	6	10	15
Tachinids	0	1	0	0
Killed by Isaria	4	4	0	0
Shrunken larvae	3	0	0	0

Apparently undecayed moss provides a more suitable overwintering medium than the decayed peat.

Drought

Drought conditions frequently occur in conjunction with high temperatures, and as a result it is often difficult to ascertain which of the two factors is operating at a given time. From evidence available, however, it appears that excessively dry conditions may exercise a greater limiting influence than high temperature in the sphagnum-covered swamps.

This was clearly illustrated in 1929 when the swamps in Itasca Park became very dry to a depth of a foot or more. High mortality occurred among the larvae seeking a suitably moist spot in which to cocoon. A large proportion of those that did succeed in cocooning penetrated deeply into the moss, where they were later covered by water and drowned. This condition resulted in the almost complete extermination of the insects in many swamps, so that in 1930 the insects needed for experiments could not be collected in Itasca Park swamps.

Throughout Michigan, summer-drought conditions prevailed from 1932 through 1937. During that period the larch sawfly almost disappeared throughout the state, and from 1936 until 1949 it was almost impossible to find specimens in any swamp.

Both in 1929 and 1930 dry, hot conditions inhibited cocooning in Itasca Park, and a very large proportion of the larvae within apparently normal cocoons were shrunken and dead; 53 percent of the prepupae observed in 1929 and 78 percent in 1930 died thus in the cocoon. In many instances the cocoons were thin, indicating that the larva had died before spinning was completed. How much of this effect was due to drought and how much to heat must remain a matter for conjecture.

In considering these physical effects it should be pointed out that seepage swamps fed by springs are seldom affected greatly by a single dry season. Only by the combined influence of several dry years will the flow from springs be affected to a point that the sphagnum mat will become dry. Iron Spring Swamp, near Itasca Park, is such a seepage. Mortality of the sawfly, though severe, was lower there than in swamps that became very dry in 1929 and 1930.

Excess of Water

In a few swamps the larch sawfly has never become abundant due to excessively wet conditions (Lejeune, Fell, and Burbidge, 1955). One such area was located near Becida, Minnesota, and one near Clarissa. Both of these swamps passed through the 1908 outbreak without appreciable injury. The latter one was later drained, about 1910, after which an outbreak of the sawfly developed. Both were seepages.

The Becida swamp is a very wet swamp where marsh marigold, Carex, and other

wet-land plants thrived wherever light was available. In such an area the sawflies could find few spots suitable for cocooning and as a result no severe infestation could build up. When surrounding sphagnum-covered swamps had been stripped bare of foliage, the Becida swamp remained green and thrifty. From these observations it seems clear that when tamarack swamps are drained, if provision is made for closing the ditches during the early spring in order to restore temporarily the original water level, the larch sawfly would thereby be controlled. In the spring of 1935 a drainage ditch was closed by Orr partly flooding a swamp near Deer River, Minnesota, causing high mortality of larvae in the parts of the swamp thus flooded. The parts of the swamp that were not flooded were sprayed by hand with an arsenical. The sawfly population was greatly reduced in 1936.

Reduction in Tree Vigor

The influence of terminal-shoot length upon the number of eggs laid per shoot has already been discussed. Also in Table 6 are presented data indicating the effect of defoliation upon the dry weight of the leaf fascicles in years following severe defoliation.

The reduction in tree vigor with each defoliation, resulting in smaller fascicles and shorter terminal shoots, acts as one of the automatic checks on the population increase of the insect. It should be remembered, however, that, under conditions existing in the Lake States between 1906 and 1914, in spite of reduced tree vigor, the outbreak continued until at least 60 percent of the tamarack over 3 inches in diameter had been killed. Evidently the sawfly population was so tremendous that even though each female may have laid a very small proportion of her complement of eggs the resultant larvae consumed all of the available needles. This situation probably can only occur when mature stands of tamarack prevail in a locality.

Competition with the European Larch Case Bearer

In Southen Michigan in 1927 the European larch case bearer was becoming firmly established and was causing severe defoliation. In Mud Lake Swamp near Ann Arbor, the insect had become established in one part of the swamp while a minor outbreak of the larch sawfly was in progress in another. Annual defoliation by the casebearer, as it spread through the swamp, added to that of the sawfly, so lowered the vigor of the trees that the abundance of the sawfly was reduced.

As the casebearer spread through Michigan toward the north, a similar reduction in sawfly numbers was observed throughout the Lower Peninsula. This apparent competition was accompanied and followed by the drought of the thirties, the effect of which was confusing, obscuring the competitive relation between the two insects. The Mud Lake Swamp instance is of particular interest because the sawfly population was reduced before drought effects became operative and therefore indicates the importance of competition with the casebearer.

Egg and Larval Mortality

Beginning in 1928 and 1929, as previously pointed out, groups of larch sawfly eggs and larvae were observed throughout their developmental period and every practicable effort was made to determine all causes of mortality.

The egg stage suffered little mortality from any cause, usually one percent or less. It seems safe to conclude that the egg stage is one which suffers little from any kind of environmental resistance under conditions existing between 1928 and 1935.

In contrast the first instar larvae were highly vulnerable to various causes of mortality, especially predators. Chrysopid and coccinellid larvae were responsible for much of this mortality, but pentatomids were occasionally observed feeding on the larvae. At times these predators may kill

TABLE 12. Mortality of exposed eggs and larvae.

Source of eggs	Year		Total eggs	Percentage of original number dying						
				Eggs	1st inst.	2nd inst.	3rd inst.	4th inst.	5th inst.	Total mortality
Mated females[1]	1928	E. larch	42	0	27	0	5	0	5	37
Mated females[1]	1928	Tamarack	575	1	34	1	7	3	5	51
Unmated females	1928	E. larch	231	0	19	8	16	16	6	65
Iron Spring	1928	Tamarack	497	1	45	1	0	2	9	58
Iron Spring	1929	Tamarack	378	10	48	6	8	6	8	86
Floating Bog Swamp	1928	Tamarack	114	4	2	0	2	7	27	42

[1]Caged with male during oviposition, then cages removed.

almost all the small larvae in a swamp.

Table 12 presents the mortality that occurred in and near Itasca Park during 1928 and 1929 while the insects were in the egg and larval stages. Although there was considerable variation, the mortality during the first instar was consistently high, whereas losses during other instars were much lower. During the 5th instar, the final feeding stage, the mortality observed was especially variable.

Because the majority of larvae parasitized do not succumb before they leave the tree at the end of the fifth instar, the effects of these organisms in bringing about mortality are not evident in Table 12. However, some idea of the influence of parasitism on the larvae may be had from studies made in 1928 and 1929 when obviously parasitized larvae in Iron Spring Swamp were kept under observation. In 1928 the larvae exhibiting dark spots indicating punctures through the integument, or with tachined eggs on their bodies, numbered 137, or 26 percent of the original egg population under observation. In 1929, 50 of the larvae under observation, or 13 percent, showed these evidences of being parasitized. Adding this mortality to that indicated in the last column of Table 12, the mortality of the groups of larvae observed in Iron Spring Swamp from all causes was 84 percent in terms of the egg population in 1928 and 99 percent in 1929. The results observed in other places deviated considerably from these.

Thus it is important to keep in mind when evaluating mortality factors that considerable variation may be expected between groups of larvae living in different swamps even in the same general locality, and still greater variability may be expected from year to year. It is evident, however, that the total mortality during the larval stage is tremendous.

Much of this loss is due to parasites and predators, but physical effects other than temperature and moisture may from time to time produce great larval mortality. The most important of these are wind and rain. Heavy storms wash larvae from the trees. Perhaps some of these find their way back to the foliage, but there is no evidence that many return. Orr observed in 1933 a case near Clarissa, Minnesota, when a heavy wind and rain removed almost all larvae from the western side of infested trees, leaving only those on the sheltered eastern sides. Similarly in Iron Spring Swamp in 1928 the number of first instar larvae was greatly reduced by wind and rain during an electric storm. It is improbable that these larvae were able to return to the trees since no larva were ever observed creeping up the trunks or along the large branches of tamarack trees.

Mortality During the Cocoon Stage

Beginning in 1924, cocoons were placed in cages set in sphagnum moss in a tamarack swamp and permitted to pass the

TABLE 13. Emergence from cocoons and mortality in cocoon.

Year of cocooning	Number cocoons	Sawflies emerged	Percentage of Total Cocoons						
			Ichneumon	Tachinid	Pteromalid	All parasites	Isaria farinosa	Other mortality	Total
1924	200	55	–	–	–	–	–	73	73
1925	646	298	–	–	–	22	22	10	54
1926	83	10	–	–	–	–	–	88[1]	88
1927	300	124	–	–	1	10	0	49	50
1928	922	191	9	6	21	36	13	29	78
1929	340	58	10	2	12	24	0	53	77
1930	816	150	1	1	0	2	0	78	80

[1]No separate record of parasites, all mortality lumped together.

winter under as nearly natural conditions as practicable. These experiments are not exactly comparable from year to year because of variations in the depth of the moss covering and variations in the manner of record keeping. They all overwintered under reasonably favorable conditions. These data are presented in Table 13. The results are expressed as percentages of the total number of cocoons overwintering each season.

For the 1930 rearings about one-half the larvae were collected late in their development and held for a few days in the insectary, until they pupated. Then they were not subject to further parasitism, either by ichneumons or tachinids. This may have affected the number of larvae parasitized, but only to a slight degree, and could not account for the very low rate of parasitism for that year.

The low parasitism, however, was offset by an increase in the effects of other factors, chiefly hot-dry weather in 1930. The data presented in Table 13 include only a part of the tachinid parasitism because the puparia of these parasites are frequently formed in the moss outside the sawfly cocoon.

Parasites of the Larch Sawfly

Three major parasites were reared from larvae and cocoons of the larch sawfly between 1924 and 1931. They were *Mesoleius tenthredinis* Morl., an ichneumonid; *Tritneptis klugii* (Ratz.) a pteromalid; and *Bessa harveyi* (Tsnd.) (*B. selecta*) a tachinid. All three of these parasites were moderately abundant, but were not numerous enough to have brought the sawfly outbreak to an end without the additional influence of other factors. From 1925 to 1930, however, total parasitism was appreciable and certainly contributed to a reduction of the sawfly population. The percentage of cocoons parasitized increased through 1929 and decreased sharply in 1930, paralleling the marked decrease in the sawfly population in the summers of 1929 and 1930. Evidently the parasite populations, together with their host, were affected by the unfavorably hot and dry weather. If starvation had been the cause of host population reduction the prognosis would have been for a sharp increase in the percentage of parasitism the year following host reduction.

In 1914 some parasites were reared from cocoons collected in Itasca Park. These were presumably destroyed while in storage awaiting identification, since none are to be found in the Minnesota insect collection. Ruggles (1910) reports the rearing of the ichneumonid *Diglochus* sp. identified by Brues. Other than this there is no specific information on the parasites present at the time of the 1908-14 outbreak. It is recalled that some ichneu-

monids were reared. The only parasite that was numerous, however, was the pteromalid, *Tritneptis klugii* (Ratz.), and most of the small size parasite emergence holes were cut by that species. Observations made in 1913 and 1914 indicated that the adults creep about through the moss in search of sawfly cocoons. When one is found, the female inserts her ovipositor through the cocoon and deposits eggs upon the prepupa within. Presumably the species is polyembryonic. The larvae feed externally upon the host, pupate within the cocoon, and all usually emerge through a single tiny, circular hole cut in the cocoon. All stages were to be found in mid-summer, and from this we concluded that there may be several overlapping generations during a season.

During the winter of 1934 and 1935, Orr reared this insect in the laboratory at room temperature and found the entire life cycle under such conditions required only from 19 to 24 days. Therefore, we may safely assume that this pteromalid produces repeated generations, the number depending chiefly upon temperature.

During the 1919 to 1929 outbreak Tritneptis was numerous, parasitising up to 21 percent of the cocoons. Generally speaking, however, it did not appear to be as abundant as it had been in 1913 and 1914.

Mesoleius adults were reared in 1928 in Itasca Park and subsequent years. Only a relatively small series found its way into the University of Minnesota collection, as most of the specimens reared were lost in the fire previously mentioned.

Records fail to disclose that any hymenopterous parasites from Europe were liberated in Minnesota. A shipment of parasitized cocoons from Dr. C. Gordon Hewitt were sent to the late H. H. Pettitt of Michigan State College on May 11, 1911. Parasites reared from these cocoons were released near Munising, in the upper peninsula of Michigan in June of that year, according to records left by Professor Pettitt.[1] Unless it is a native species, the population of *M. tenthredinis* now present in Minnesota must have spread either from Manitoba or from northern Michigan.

The percentage of parasitism by this insect was never extremely high either in Itasca Park or other parts of Minnesota. In 1928 nine percent of the cocoons yielded large ichneumonids, for the most part Mesoleius, in 1929 ten percent and in 1930 only one percent.

By far the most abundant parasite during the 1919 to 1929 outbreak in Minnesota was *Bessa harveyi*. This tachinid emerged from thirty-seven percent of the overwintering cocoons in 1928, thirty percent in 1929, and four percent in 1930 when the host population had been reduced to a low level. These percentages represent only a part of the larvae parasitized by this insect because some of the host larvae are killed before cocooning and, as previously mentioned, some of the maggots leave the cocoons and form their puparia in the moss outside the cocoon of the host.

In 1928, fourth and fifth stage larvae that displayed external evidence that they had been parasitized were separated from the others and fed until they either died or spun cocoons. In the fall the cocoons were slit open carefully and those containing living larvae were held over winter under two inches of sphagnum moss under natural conditions, permitting both host and parasites to continue development.

Evidences that the larvae had been parasitized were the presence of tachinid eggs on their bodies or necrotic spots indicating that the body wall had been punctured by an entering larva or the ovipositor of some parasite. It was suspected when this experiment was begun that the puncture marks might have been made in large part by ichneumonids, but results demonstrated that most of them were caused by entering tachinids, as shown in Table 14.

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[1]Information furnished by Dr. Walter Morofsky.

TABLE 14. Fate of obviously parasitized larvae.

Evidence of parasitism	Number total larvae	Percentage of parasitized larvae killed: Dead & mummified	Isaria farinosa	Other micro-organisms	Others dead in co-coons	Tachinids	Ichneumons	Pteromalids	Sawfly adults
Punctured	134	8+	10	30	0	39	1	7	5
Tachinid eggs	40	33	5	25	12	17	3	5	0
Eggs & punctured	18	6	0	33	0	50	0	5	6
Mean percentage		12	8	30	2	37	1	6	4

Many parasitized larvae actually die from causes other than parasitism. Twelve percent of those attacked by parasites became mummified within the cocoon, probably as a result of unfavorable physical conditions. This figure compares closely with the percentage of mummified individuals among the unparasitized larvae from which the parasitized part of the population was separated, i.e., fifteen percent. A small proportion, eight percent, was killed by the parasitic fungus *Isaria farinosa*. Other unidentified microorganisms destroyed thirty percent of the parasitized larvae. Elimination of tachinid eggs through moulting was observed and it seems likely that some parasites were overcome through encapsulation of *Mesoleius* eggs (Muldrew, 1953, 1955). This matter of the total influence of parasites deserves further intensive study.

Much more work is needed before life tables for the larch sawfly comparable with those of Morris and Miller (1954) for the spruce budworm can be formulated (Lejeune, 1955). We may expect that the detailed resistance components reducing the sawfly populations will never twice be exactly the same. But with so many factors operating simultaneously it seems likely that when the force of one declines, another will arise to take its place except where forest conditions are especially favorable for the pest. Only then are disastrous outbreaks to be expected.

One thing is clear. Only a single tachinid fly can be produced from a single host regardless of the number of eggs deposited on a larva. These may number eight or more. The puparia are usually formed within the host cocoon but a few *B. harveyi* larvae emerge from their host before the cocoon has been formed, whereas others may leave the cocoon before transforming to the puparium. Thus every condition may be observed from mortality of both host and parasite, in cases of multiple parasitism, when larvae younger than the fourth instar are attacked, to the successful completion of parasite development culminating in the emergence of an adult fly from its puparium.

Thus, in evaluating the correct effect of parasitism upon a population, those parasitized hosts that are killed by the parasite before cocooning should be included with those from which parasites actually emerge in order to show the true influence of the parasites. On the other hand, parasitized larvae that are killed by other resistance forces before the effects of parasitism are evident should not be credited to the parasite. Unless the entire picture of parasite-host coaction is understood there is always danger of misinterpreting results.

Obviously conclusions based only on rearing parasites from cocoons are erroneous, especially for tachinids such as *Bessa harveyi*. Even for ichneumonids, the rearing procedures may not be as accurate as dissection in giving a true value for the number of hosts attacked by parasites. On the other hand, dissections do not disclose the proportion of parasitized larvae that

TABLE 15. Fifth instar larvae apparently parasitized.

Year	Location	Total number larvae	Tachinid eggs No.	Tachinid eggs percent	Punctured No.	Punctured percent	T. eggs & punctured No.	T. eggs & punctured percent	Percent apparently parasitized
1928	Fl. Bog Bay	154	27	18	9	6	6	4	28
1928	Iron Sp. Swp.	536	69	13	234	43	49	9	65
1928	Unidentified	288	26	9	145	50	17	6	65
1929	Iron Sp. Swp.	209	61	29	17	8	18	9	46
1931	Upper Fl. Bog Bay Swp.	141	51	36	0	0	7	5	41
1931	Arago	411	57	14	2	0.5	7	2	16

would die from other causes. In spite of the weaknesses that are apparent, counts of punctured and egg-bearing larvae made in the field can give a relative idea of parasite trends from season to season and place to place.

The results of a series of such counts, recording separately the number of larvae with tachinid eggs cemented to their bodies, the number with necrotic spots, and the number with both are presented in Table 15. The percentage varied greatly from swamp to swamp and from year to year, and the percentages of parasitism indicated were appreciably higher than those based on emergence from the cocoons, as would be expected.

Since the proportion of ichneumonid parasites was always relatively low, it may be assumed that the greater proportion of the punctured larvae on which Table 15 is based were attacked by *Bessa harveyi*. The variations from year to year and from place to place are shown in the last column.

Vertebrate Predators of the Larch Sawfly

A variety of vetebrates feed more or less upon the larch sawfly, but except for certain small mammals most of them are too few in number to have much influence on the sawfly population. Birds, in the course of our studies, have only occasionally been observed to feed upon the sawfly larvae. Specifically the chipping sparrow and the yellow warbler were seen eating this insect in and near Itasca Park on a few occasions. Doubtless other species also took sawfly larvae from time to time, but the number destroyed by birds was negligible. More recently others (Buckner 1953) have observed swamp sparrows, several species of warblers, and evening grosbeaks feeding upon the sawfly larva.

Mammals, on the other hand, exercise an influence upon the sawfly that is often tremendous. Skunks are especially fond of larch sawfly cocoons and dig them out of the moss at times of high sawfly numbers. The presence of sawfly cocoons in the droppings of these animals is a common occurrence during outbreak periods. However, the skunk population is usually not sufficiently high to affect the sawfly numbers appreciably.

At times frogs may consume considerable quantities of larvae dropping from the trees to pupate. Unpublished data furnished by William Marshall that were collected in Upper Floating Bog Bay Swamp, in Itasca Park, show that in 1953, wood frogs consumed large quantities of larvae. Thirty-three of forty-seven frog stomachs examined contained sawfly remains and constituting 56 percent of the food items. In terms of bulk this percentage would be higher, since most items of animal food were smaller in size than the sawfly larvae. The average number of larvae per frog was 4.6. Marshall estimates that the number of frogs per acre in the swamp between 1949 and 1952 ranged between

100 and 554 per acre. It would be interesting to know how many larvae a frog will eat in a given time, so that the influence of these animals in reducing the sawfly population might be estimated. Buckner (1952) has also reported predation of larch sawfly by frogs.

Small mammals, especially mice and voles, destroy tremendous numbers of sawfly prepupae. The observations concerning these animals made in both Itasca Park and Michigan through the summer of 1928 have been published (Graham, 1928) and need not be repeated. Since that time, however, further observations have been made which clarify certain points in the coaction between the sawfly and small mammals. These points will be mentioned briefly.

Voles, especially *Microtus pennsylvanicus*, deer mice, *Peromyscus maniculatus*, and two species of shrew both in Minnesota and Michigan have regularly been trapped in snaptraps baited with sawfly cocoons. Evidence points to the voles as being the most active and effective group of larch sawfly predators.

Whether or not shrews actually eat sawflies in the cocoon stage has not been directly demonstrated although it has been assumed on the basis of indirect evidence that they do. Stomach examination of animals trapped failed to reveal either head capsules of the sawfly or parts of cocoons, whereas the stomachs of voles captured at the same time were filled with insect fat. The teeth of shrews, being of the insectivorous type, do not seem to be well suited to opening the tough sawfly cocoons, although they probably could tear through the cocoon wall. No such torn openings have been observed in any of the hundreds of cocoons examined during the present study.

Another point that has been clearly shown by cocoon collections in Mud Lake Swamp, near Ann Arbor, is that feeding activities are greatest in early autumn but continue through the winter. For example, during the fall and winter of 1928-29 65 percent of the cocoons had been opened by mice or voles in September. In October the percentage had increased to 66 percent. Little additional feeding occurred during the winter, as indicated by an April collection, but in May the percentage opened had increased to 70. After deducting mortality caused by other factors, there remained only 6 percent of the cocoons containing normal prepupae. These observations suggest that feeding by voles upon the sawfly cocoons was intensive in the early fall, light during the winter, and accelerated somewhat in May.

It is to be expected that the activity of small mammals in opening sawfly cocoons will vary from place to place depending upon the abundance of both the cocoons and the mammals. At peaks of vole population the easily accessible cocoons might all be taken during early fall, whereas feeding would continue later when the sawfly was fed upon by a smaller number of the mammals.

Still another point was brought out by the data collected in Itasca Park in 1931. They show that voles rejected cocoons containing dead or parasitized larvae. At that time Orr repeated the experiments already reported (Graham, 1928), planting sawfly cocoons in cheesecloth bags at regular intervals in places where they might normally be expected to occur. In addition to the plots previously used in the 1927-28 experiments he set out cocoons on all Itasca Park larch sawfly plots, more than doubling the number of areas sampled. Three apparently normal cocoons were enclosed in a cheesecloth bag and covered with about two inches of moss. A portion of the cocoons were accidentally crushed by the shrinking of the bag. Some bags thus contained cocoons with dead or parasitized larvae. Whenever a bag was disturbed by mice or voles all the cocoons were usually removed therefrom. In 16 instances, some cocoons were rejected in bags from which others had been taken.

In every such instance the larvae within the cocoons that were rejected were dead on examination.

The proportion of cocoons containing dead larvae differed greatly from plot to plot. The greatest mortality occurred on the wettest plots. On these plots sedges and mosses had not grown to a point where hummocks suitable for cocooning had developed, and the general level of the surface was little above the normal water level, conditions definitely unfavorable for both sawfly hibernation and for small mammals.

In 1931 the population of sawflies in Floating Bog Bay Swamp was very low. One would expect therefore that the voles would pay little attention to this relatively scarce source of food. However, the percentage of the planted cocoons that were opened was as high as in the earlier experiment in 1927 when the sawfly was abundant, the percentage opened by mice or voles ranging between 30 and 80 percent. It must be concluded, therefore, that where these animals are numerous they will find sawfly cocoons in the course of normal searching for food, and that the proportion opened bears a closer relation to vole abundance than to the density of the sawfly population.

In addition to the cocoon stations located on the plots referred to above, a series of 54 bags, each containing three cocoons, was set out at regular intervals across Upper Floating Bog Bay Swamp. The proportion opened varied in different parts of the strip. On the forested high ground adjacent to the swamp only 5 percent of the bags were disturbed, whereas in the swamp marginal zone the number opened was 44 percent and within the swamp 35 percent. These figures correspond with the relative vole population that would normally be expected to occur in the three locations, and suggest that these animals may exercise a greater influence upon the sawfly than do mice, which are more numerous in upland woods than in the swamps.

Summary of Mortality Factors

The most obvious points brought out in this discussion of sawfly mortality factors may be listed as follows:

1. The eggs are subject to little environmental resistance, although at times they may be attacked by small Hemiptera.
2. The first instar larva is especially vulnerable to the effects of heavy storms and various predators, especially chrysopids, coccinellids, and pentatomids.
3. The most numerous parasite observed during the 1919 to 1929 outbreak was *Bessa harveyi*, a tachinid which exercised a conspicious influence in checking the increase of the sawfly in many places.
4. Although birds occasionally feed upon sawfly larvae, their feeding has little effect on the sawfly population.
5. Frogs feed freely upon larvae on the ground after they have dropped from the trees to cocoon.
6. Small mammals, especially mice and voles, exercise a conspicious influence on sawfly numbers.
7. Although biotic factors had a marked influence on sawfly numbers, the 1919 to 1929 outbreak was brought to an end by the effects of hot, dry weather, which, in addition to direct injury to the larvae, caused the survivors to coccon below the normal spring water level. There they were drowned before they could emerge as adults.
8. Excessively wet conditions on the swamp surface interfere seriously with successful sawfly pupation.

Resistance Factors and Larch Sawfly Population

Forest entomologists are primarily concerned with the rise and fall of noxious insect populations. Assuming that the reproductive potential of any species is characteristic of that species, it follows that environmental resistance must control the rate at which the insect will increase or decrease in number. Therefore, a thorough understanding of the forces involved must be the key to forest insect control.

When forces of resistance discussed in the foregoing pages are considered in toto the picture comes into focus, and we begin to see the relation of the parts to the whole.

Also we become more aware of the environmental complexities involved. Furthermore, it becomes apparent that some factors that have received little attention may exercise a greater influence upon sawfly populations than some that have been measured over and over.

For example, the pre-natal forces that operate to reduce the fecundity of the females deserve far more consideration than they have received. These fall into two categories: Those that influence the number of eggs that can fully develop, and those that affect the number of eggs that are actually laid. Apparently malnutrition may influence the population trends almost as much as outright starvation by its effect upon fecundity. Furthermore, even though a female may develop her full complement of eggs, none or very few may be deposited unless conditions favoring oviposition are present.

Once the eggs have been deposited, the mortality during that stage proved to be inconsequential under conditions existing during the seasons observed. Nevertheless, the fact that ten percent of the eggs were destroyed by an unidentified hemipterous nymph in one set of observations suggests that under the right combination of circumstances mortality from that cause might exercise considerable influence upon the population trends of the larch sawfly.

Factors operating during the larval and pupal stages have received special attention from all who have studied the larch sawfly, and all agree that the greatest mortality during these stages occurrs during the first instar and the cocoon stage.

The data presented herein show that the correct evaluation of these losses demands much more information than has usually been collected in such studies. For example, it is apparent that daily and detailed observations of the larvae from the time they hatch until they cocoon is needed in order to determine with certainty the relative importance of the various causes of mortality. The influence of storms, extremes of temperature, predatory organisms, and other resistance factors that operate in such ways as to leave little or no direct evidence of their work must be seen in operation if our conclusions concerning them are to be reliable. All too often this aspect of forest insect research has been neglected because observers have been too few or have been too absorbed in collecting more easily measured quantitative data.

Correct evaluation of resistance factors demands that techniques be used that measure an effect in its entirety. For instance, in this study it was shown that some parasitized larvae die before cocooning and that in the case of *Bessa harveyi* a considerable proportion of the parasite larvae may leave the cocoon to pupate. Thus the determination of parasite effects from cocoons alone cannot be reliable. Furthermore, evidence indicates that some individuals, although parasitized, may survive. Recent publications from the Canadian Forest Insect laboratory at Winnipeg (Muldrew, 1953, 1955) describe how this is accomplished and the mechanism by which the sawfly larvae protect themselves against *Mesoleius tenthredinis*. But observations in Minnesota suggest that some larvae may survive the attack of other parasites, specifically *Bessa harveyi*. These facts show that many determinations of the percentage of the larvae parasitized, based on emergence from cocoons, provide only relative values for these factors.

Evidence taken from the annual-ring pattern of tamarack demonstrated that this tree has apparently suffered repeated attack by defoliators, presumably the larch sawfly. Frequent periods of defoliation follow one another in close succession, but from time to time there are breaks lasting twenty years or more when the rings indicate that no defoliation occurred. These must represent times when the sawfly population reached very low numbers, more or less comparable with the low levels that were observed between 1929 and 1950 in Michigan.

This last low-population level was definitely the result of dry, hot weather that either killed the larvae directly or forced them to descend for pupation beneath the winter and spring water level during a series of hot-dry years. If judgment is based upon the evaluation of the facts at hand, the conclusion must be reached that weather conditions that result in alternately wet and dry conditions in the swamps are among the most potent influences restricting the sawfly population growth. Also swamps that are continually wet are unfavorable for the insects. Thus, in general, during early stages in forest succession when the tamarack grows on a very wet substratum, severe defoliation is unlikely to occur because conditions are not ideal for the cocoon stage. Therefore disastrous outbreaks are separated by the time required for the unfavorable wet-swamps, in which young tamarack has been established, to develop to a stage favorable for the sawfly, with trees of polesize or larger and great sphagnum mounds above the high-water level. Since few swamps in the Lake States are at present in this stage, the time is not ripe for a generally severe and widespread outbreak such as that which killed the tamarack forest around 1910. Frequent minor outbreaks that will reduce growth rate but will not kill many trees may be expected in the immediate future.

What Information is Needed

Although further study will doubtless disclose new facts, the basic information concerning the life history and the relations of the larch sawfly to its physical and biotic environment are reasonably well understood. Much information presented in this paper has been verified during recent outbreaks in Minnesota and Canada (see bibliography).

Therefore, the question of what further work is most likely to be fruitful may well be asked. It is doubtful if a repetition of observations already made will add much to present knowledge unless they are tied together as parts of a unified whole. The application of the so-called "community approach" to the problem seems essential to further advancement in the study of this insect. All aspects of the problem should be studied simultaneously by a group of competent workers. Such a group should not be a number of independent specialists, but a team under the supervision of a single individual. He will be the key to success. He must be a person with constructive imagination whose training, experience, and interest are such that he can view the program as a whole, and see how the various pieces fit together. He should be able to recognize when enough information has been obtained concerning one angle and when more is needed in another.

Morris and Miller (1954) in their work with the spruce budworm for which they have developed life tables are using the community approach and are expressing the effects of various resistance factors in comparable terms. A similar attack upon the larch sawfly problem might go far to demonstrate the universal value of this method of attack in the study of any forest insect.

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